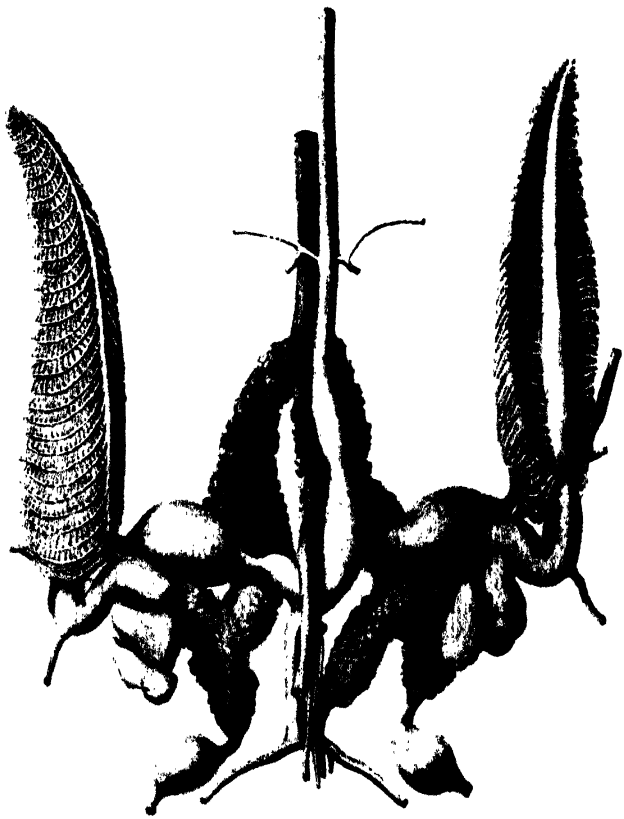
L.M.B.C. MEMOIRS

XXXII.

SEPIA



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Photographic reproduction of the original figure of the injected circulatory and respiratory organs of *Sepia officinalis*, as drawn by W. Bell in 1787, under the direction of John Hunter, who made the dissection. This drawing was first engraved and published in 1823. It represents the first detailed and accurate figure of the anatomy of a Cephalopod. The published figure has been extensively copied, but in nearly all cases inaccurately. A key and anatomical explanation are given in text figure 5. The specimen and drawing are still preserved in the Museum of the Royal College of Surgeons.

DEPARTMENT OF OCEANOGRAPHY, UNIVERSITY OF LIVERPOOL

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY
R. J. DANIEL, D.Sc.

XXXII.

SEPIA

BY

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(With Frontispiece and 24 Plates)

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EDITOR'S PREFACE

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the fauna and flora of the Irish Sea.

Dredging, trawling and other expeditions, originally organised by the Committee, have been carried on intermittently since that time, and a considerable amount of material has been accumulated.

Five volumes on the fauna and flora of Liverpool Bay have been issued and a Manx Marine Fauna List was published in 1937. The latter contains complete data with regard to the distribution and breeding of all marine animals recorded from waters about the Isle of Man, except the seals and Cetacea. In this List past records, commencing with those of Edward Forbes, have been brought up to date, and new additions have been made as a result of intensive study of the shore fauna by members of the Port Erin Biological Station staff, with the collaboration of visiting biologists.

The papers in the present series, started in 1899, are quite different from the publications mentioned above, in name, in treatment and in purpose. Each Memoir treats of one type and is issued separately when ready.

Under the guidance of the late Sir William Herdman, the founder of the series, the Memoirs assumed a definite format and character, and they became well known as aids to the study of British marine animals and plants.

Consequently, when the Liverpool Marine Biology Committee ceased to exist and the management of the Biological Station at Port Erin, erected under its auspices, was transferred to the Oceanography Department, University of Liverpool in 1920, the name "L.M.B.C. Memoirs" was retained.

The forms selected are, as far as possible, common Irish Sea animals and plants of which no adequate account already exists in the text-books.

We are indebted to the *Royal Society* and to the *Research Board, University of Reading*, for grants towards the publication of the present Memoir *Sepia*.

These grants were obtained through the services of Professor F. J. Cole, F.R.S., who collaborated with the late Professor J. Johnstone in the production of L.M.B.C. Memoir VIII, Pleuronectes, and has always shown a practical interest in the series.

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No. XXXII. SEPIA

BY

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CONTENTS*

[NOTE:—*For the sake of brevity, blood supply and innervation have not usually been included in the description of individual organs and systems. Reference should therefore be made to sections X and XIII entitled CIRCULATORY SYSTEM and NERVOUS SYSTEM.]

INTRODUCTION

Before the anatomy of the cuttlefish can be understood, it is necessary to know something of the basic organisation of the Phylum Mollusca, and also of the class Cephalopoda.

The diversity of organisation among the six recent Classes of the Mollusca, viz. the Cephalopoda, the Gastropoda, the Lamellibranchiata, the Scaphopoda, the Placophora, and the Solenogastres, is so great that the features which unite them are somewhat obscured. These features are best described with reference to a hypothetical primitive Mollusc, which illustrates what is called the molluscan plan of organisation. All the recent classes of the Mollusca show some degree of conformity to this plan.

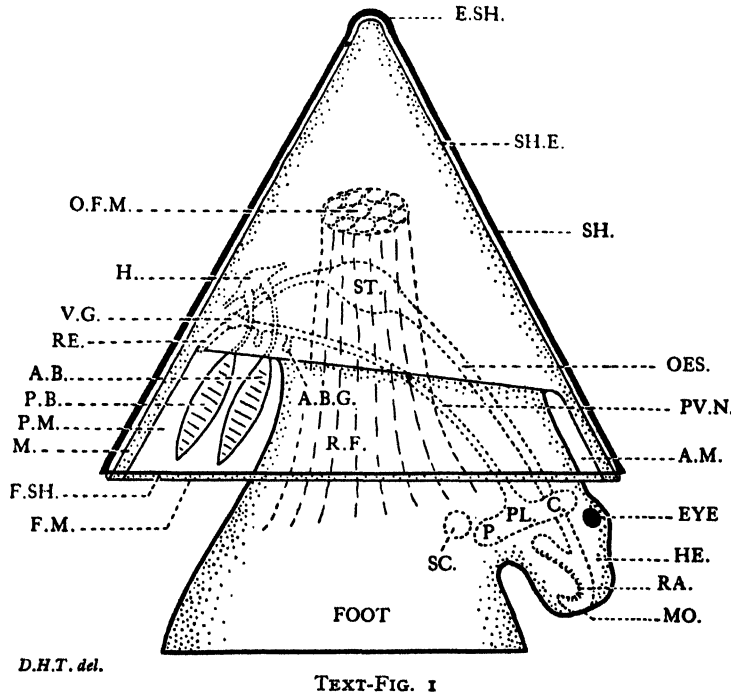
The structure of this hypothetical Mollusc has been deduced, partly from embryological evidence, and partly from the structure of the simpler members of the phylum. No pretensions are made, however, that it represents an actual reconstruction of the common ancestor of the recent classes.

Text figure 1 shows a lateral view of this Mollusc. It is bilaterally symmetrical, and has an external shell (SH.), conical in shape, and dorsally situated, the apex of which represents the embryonic shell (E.SH.). The shell is secreted by the shell epithelium (SH.E.), which is reflected back internally from the margin of the shell (F.SH.) as the mantle epithelium. This lines an annular mantle cavity (P.M. and A.M.), between the mantle (M.) itself, which constitutes a sort of cloak of soft tissue lying within the shell, and the central mass of the animal.

The mantle cavity communicates freely with the exterior. It may be regarded as consisting of an anterior and a posterior chamber, connected on either side of the foot by lateral grooves. The posterior part of the mantle

cavity contains two pairs of plume-like ctenidia (A.B. and P.B.), and the anus. The uro-genital ducts (not figured) open at the base of the ctenidia.

The ventral part of the body consists of a head region (HE.), and a large muscular foot (FOOT), which is an organ of locomotion. The foot is attached to the shell by a pair of retractor muscles (R.F.), which pass on either side of the



TEXT-FIG. 1

Hypothetical primitive Mollusc:—Lateral view to show the essential features of molluscan organisation. The figure represents a diagrammatic transparency. (Adapted from Naef.)

centrally situated visceral mass. The head and foot can be withdrawn within the mantle cavity, so that the conical shell completely covers and protects the animal, as in the case of the common limpet, *Patella vulgata*.

The head bears the mouth (MO.) and a pair of eyes (EYE). A fleshy structure called the odontophore, projects within the mouth, and supports a rasping organ, the radula (RA.).

The alimentary canal consists of the buccal cavity, oesophagus (OES.), stomach (ST.), intestine (RE.), and a posteriorly situated anus. A pair of digestive glands (not figured) open into the stomach.

D.H.T. del.

TEXT-FIG. 2

Section through the shell and mantle; to show how, in some Molluscs, the mantle may grow over the margin of the shell, partly or completely enclosing the latter.

The vascular system includes a simple heart (H.), surrounded by a pericardium. The pericardial glands (not figured), renal in function, are situated close to the heart and communicate with the pericardial cavity.

The nervous system is characterised by a system of three pairs of ganglia, the cerebral (C.), pleural (PL.), and pedal (P.), which are connected by commissures and form a ring of nervous tissue round the oesophagus. A prominent pleuro-visceral nerve (PV.N.) runs from this ring to the posterior end of the body. Text figure 1 also shows the visceral ganglion* (V.G.) and two branchial ganglia (A.B.G. and unlettered). There are a pair of statocysts (SC.) situated close to the pedal ganglia.

Class CEPHALOPODA

Recently the classification of the Cephalopoda has undergone considerable modification, due largely to the work

*This ganglion corresponds to the posterior visceral commissure and not the visceral ganglion of *Sepia*. The pleural ganglion corresponds to the visceral ganglion of *Sepia*.

of Naef and other German zoologists. An outline of the classification of the Cephalopoda is given on page 15. This is taken from Grimpe (1922). The similarity of the structure of the shell of *Nautilus* to that of the Ammonites, though not complete, is sufficiently remarkable to justify these two groups being placed in the same subclass. It is unlikely, however, that it will ever be established whether the Ammonites really were tetrabranchiate, so the compromising words Dibranchiata and Tetrabranchiata have been dispensed with, and Metacephalopoda and Protocephalopoda substituted.

The Class has very well-defined characteristics, but like the other Classes of the Mollusca, it has undergone profound modifications from the primitive molluscan plan. Text figure 3 shows a median longitudinal section of a hypothetical primitive Cephalopod, constructed in the same way as in the case of the hypothetical Mollusc. Comparison with Text figure 1 shows that in spite of far-reaching modifications, the essential molluscan organisation is not completely masked.

There is a prominent head, bearing a pair of well developed eyes, and the anterior part of the molluscan foot is modified to form circumoral appendages (CI.AP.), while the posterior part forms the exhalent funnel (F.). The very large posterior chamber (P.M.) of the mantle cavity contains two pairs of branchiae (unlettered and P.B.), and the renal, reproductive (unfigured) and anal (AN.) apertures. The mouth is provided with a pair of powerful horny jaws (D.J. and unlettered) and an odontophore is present.

The primitive cephalopod shell, called the phragmocone, is conical in shape, but the apical region has been partitioned off by septa into a series of chambers (C.PH.) pierced by a slender tube (SI.), called the siphuncle. The animal only occupies the last chamber (L.CH.).

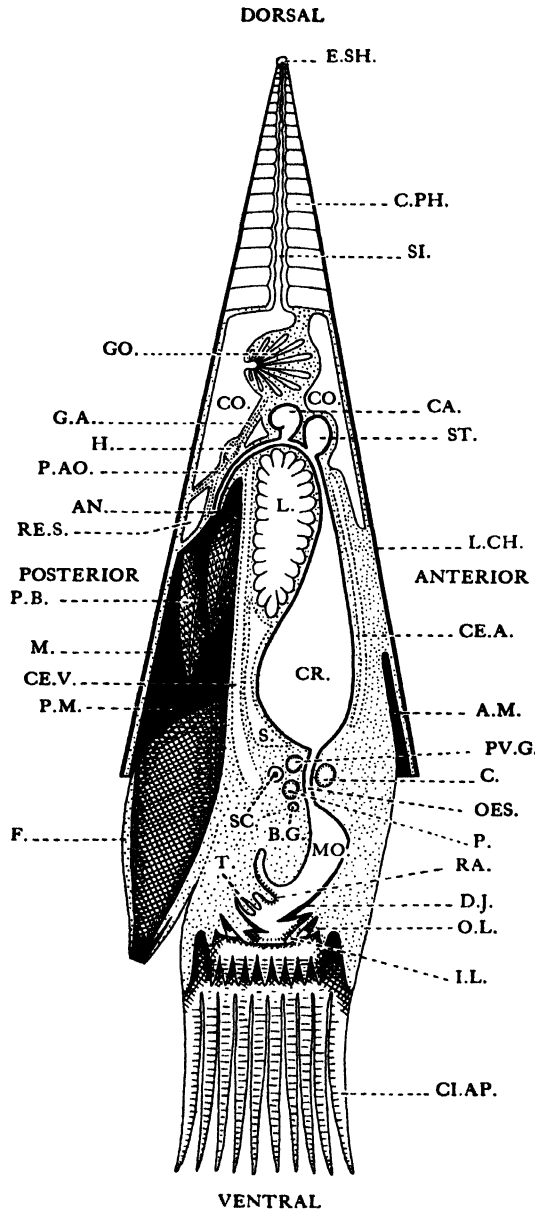
The alimentary canal includes a crop (CR.), stomach (ST.) and a caecum (CA.), and there are a pair of very large digestive glands (L.). There is an extensive coelom (CO.) in which the gonads are located.

The vascular system is highly developed, and includes a heart (H.), a system of veins and arteries, and blood sinuses. The renal organs consist of glandular diverticula of the venae cavae.

The main nervous ganglia, the cerebral (C.), pleuro-visceral (PV.G.) and pedal (P.), are concentrated in the head, forming, with their commissures, a ring round the oesophagus (OES.). There are paired statocysts (SC.), and paired olfactory pits, the latter situated dorsally to the eyes on the surface of the skin.

Morphologically, the orientation of this Cephalopod is such that the apex of the shell is dorsal, the mouth ventral, and the main mantle cavity posterior. The normal, i.e. physiological body position of Cephalopods is however, so very different from this, that, except when comparing them with other Molluscs, to persist in using it is only confusing. Nowadays the physiological orientation, based on the position occupied by many Cephalopods, especially in swimming, has been adopted. According to this standard, the mouth is anterior, the apex of the shell posterior, and the main mantle cavity ventral.

Although they are essentially molluscan, the organisation of the Cephalopods is far above that of the other Classes. They include not only the most highly organised, but also the largest invertebrate animals, varying in length from less than two inches to over fifty feet. In distribution they are entirely marine. Palaeontology shows that the recent species, considerable though they are, can only be regarded as survivors of a group which has long since passed its prime; but neither palaeontology nor embryology has provided any clue to their origin, and the



D.H.T. del.

TEXT-FIG. 3

Median longitudinal optical section through the body of a primitive hypothetical Cephalopod, to show the essentially molluscan organisation. Morphological orientation: compare with text figure 1. (Adapted from Naef.)

profound modifications in development, with the absence of the free larva, due to the enormous yolk supply in the eggs, is yet another feature which isolates them from the other members of the Phylum.

Sub-Class METACEPHALOPODA (DIBRANCHIATA)

This sub-class consists of Cephalopoda in which the shell, when present, lies entirely within the body (except in *Argonauta* and *Spirula*). The ventral part of the primary mantle (Text figure 4 (*a*), PR.M.) and shell of the phragmocone inhabited by the animal has been replaced by a muscular mantle wall (Text figure 4 (*b*), M.M.).

There are only 8 or 10 circumoral appendages, or arms, which, at least in youth, bear suckers. The eyes are highly developed, each consisting of an enclosed capsule, provided with lens and iris, lying in an orbit. There is only one pair of ctenidia or branchiae, in whose axes lie branchial glands, each of which is fastened to the mantle for the greater part of its length by a branchial ligament. The funnel forms a complete tube, through the union of its two halves in the mid-ventral line, and is partly lined with a glandular epithelium, the funnel gland. An ink gland and duct are present. The skin contains chromatophores, which make remarkable colour changes possible. Paired poison glands, often called salivary glands, open into the mouth.

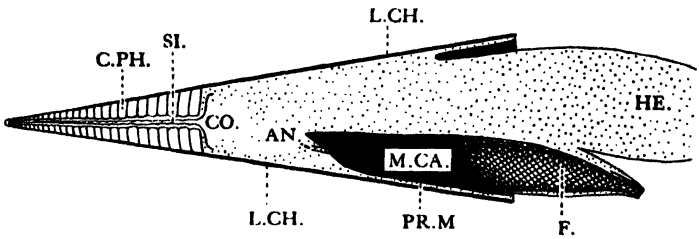
The above features distinguish the recent Metacephalopoda from the Nautiloidea, which are the only recent members of the Protocephalopoda. Among the Metacephalopoda there is very great uniformity of structure.

Order *DECAPODA*

This order consists of Metacephalopoda in which there are ten arms, two of which are modified to form tentacles

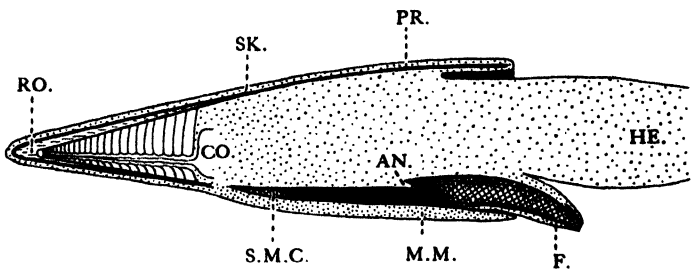
TEXT-FIG. 4

Diagrams of median longitudinal sections through the bodies of certain hypothetical cephalopod types, to illustrate the evolution of the Sepia Shell. (Adapted from Naef.)



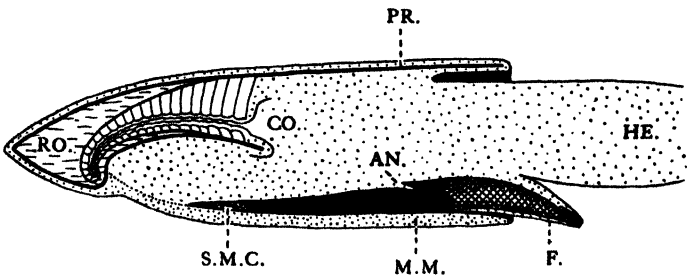
D.H.T. del.

(*a*) ***Primitive Cephalopod.*** This represents the first stage in the advance from the primitive cone-shaped molluscan shell. It consists of a simple phragmocone, which is radially symmetrical and external. The animal occupies only the terminal chamber.



D.H.T. del.

(*b*) ***Primitive Decapod.*** The shell has lost its radial symmetry and is internal. The rostrum has been added, which continued forwards as the proostracum, takes the place of the dorsal wall of the terminal chamber. The ventral wall of the latter, and the primitive mantle attached to it, have been replaced by the "muscular" mantle.



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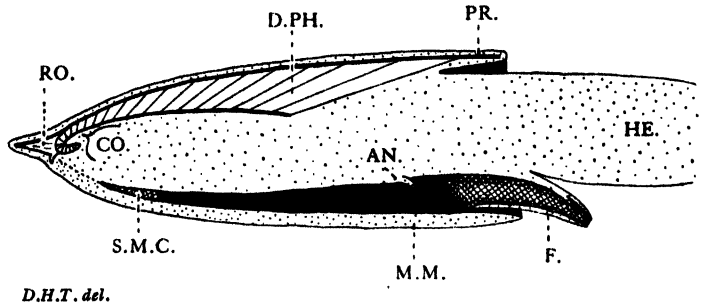
(*c*) ***Primitive Sepioidea.*** The rostrum is more highly developed; the phragmocone is bent in ventrally. The muscular mantle is attached to the outside of the shell.



(*d*) *Sepiidae*. The rostrum, the proostracum, and the ventral part of the phragmocone are vestigial; the septa of the dorsal part of the latter, which is highly developed, slope obliquely.

in which the suckers are limited to a club-like portion at the distal end. The suckers are stalked, and have horny rims which may be remodelled during development to form hooks. A well-developed shell is present. The renal apertures have been displaced away from the bases of the branchiae towards the anus. A fold of skin, called the buccal funnel, which surrounds the mouth, is connected to the bases of the arms by 6 to 8 pieces of radial webbing called buccal pillars. On either side of the funnel there is, except in the Cranchiidae, a cartilaginous disc into which a corresponding structure on the mantle wall fits, the two forming a locking mechanism.

Sub-Order SEPIOIDEA

In this Sub-order the phragmocone, where it has not been lost, is bent in ventrally at the posterior end, and its ventral free margin is pushed into the body. The muscular mantle is thus attached to the outside of the shell. In the primitive Sepioidea (Text figure 4 (*c*)) the shell consists of a phragmocone, embedded in a well developed rostrum (RO.), which is produced forwards to form the proostracum (PR.).

Family SEPIIDÆ

In this family the dorsal part of the phragmocone (Text figure 4 (*d*), D.PH.) forms a compact stratified cuttlebone, the septa of which are inclined obliquely towards the antero-posterior plane, and the ventral half of the phragmocone and the siphuncle are vestigial. The proostracum has been replaced by continuations of the wings of the shell (Figure 15, H.SH. and C.SH.), and the rostrum is either reduced or absent (Text figure 4 (*d*)). The body is dorso-ventrally compressed, but comparatively broad, and the fins do not meet at the posterior end of the body.

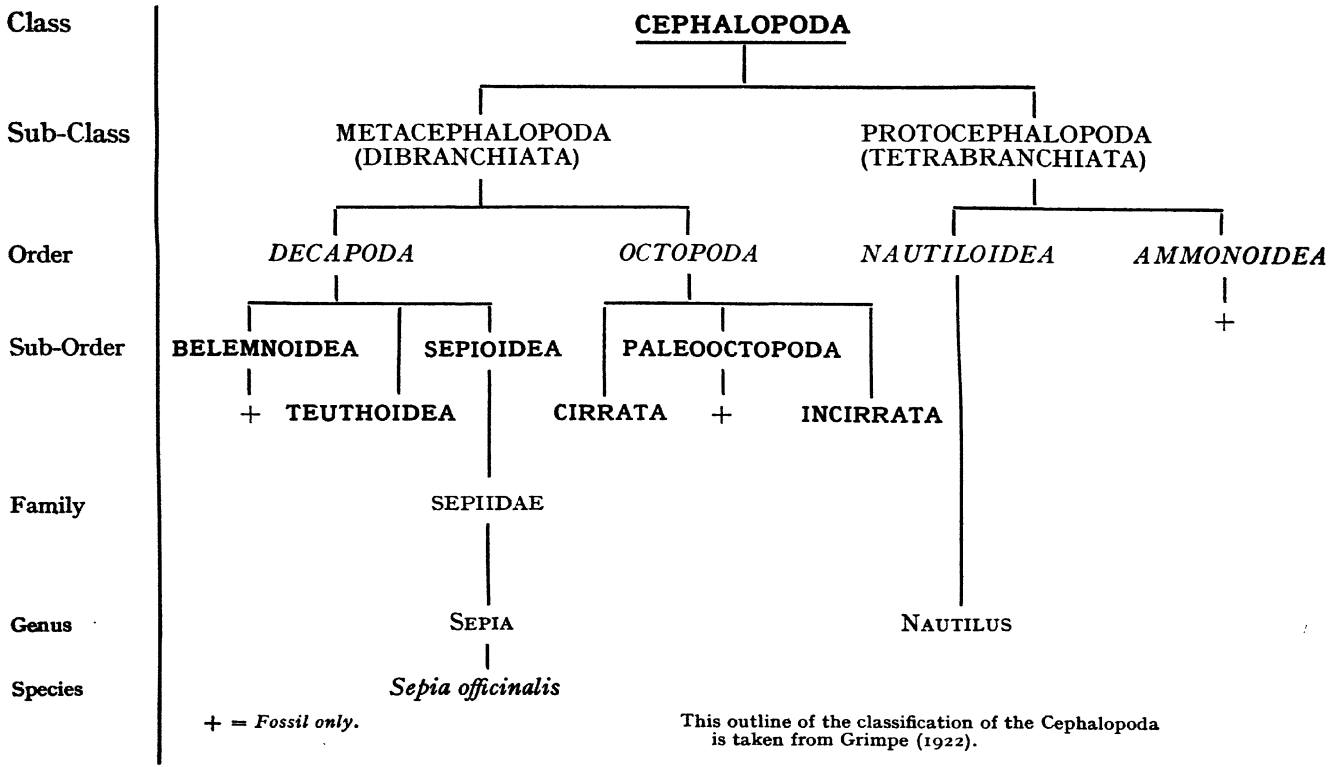
In the classification of the Decapoda great attention has been paid to the shell. This not only makes it possible to link up the recent forms with vast numbers of fossil Decapods, of which the shell only is preserved, but also helps to provide a solution to the problem presented to the systematist by the very great uniformity of structure within the order.

HISTORICAL.

The first reference to the cuttlefish appears in Aristotle's "Historia Animalium" (c. 330 B.C.).

Aristotle's account was concerned chiefly with its habits. He considered the cuttlefish a very cunning animal and observed that the ink supply was more abundant than in the case of the octopus. He recorded that *Sepia* ejected ink not only when afraid, but also used an ink cloud to hide in, both to escape from fishermen, and also when lurking in pursuit of prey.

He says that when a female is caught, males come to her rescue; when on the other hand, a male is harpooned,



This outline of the classification of the Cephalopoda is taken from Grimpe (1922).

the females flee. This behaviour he interpreted as indicating courage and love on the part of the male.

He describes the nidamental glands in the mantle cavity of the female, but regarded them as resembling teats.

He also includes observations concerning differences of colour between the male and female, egg-laying and fertilisation, and the duration of life which he puts at less than two years. A point of special interest in Aristotle's observations on the Cephalopods is his mention of the hectocotylus, which was not re-discovered till comparatively recent times.

The first scientific account of the anatomy of the cuttlefish was given by Swammerdam (c. 1675). This appears in a letter to his friend Redi, published in the Biblia Naturae (1738) fifty years after Swammerdam's death. He called the cuttlefish *Sepia maris* or the Spanish sea-cat. Swammerdam refers to the "innumerable fallacies and dreadful errors which throughout the ages have crept into the writings of the earlier authors," and appeals to the student of nature to go to the animal itself for his facts, and not to rely on books alone. Unfortunately he does not indicate to what writings he refers, but, judging from the anatomical mistakes which Swammerdam himself made, and his confusion over the interpretation of some of the organs, these earlier writings cannot have much significance.

He attacks the avarice of the fishermen from whom he obtained his material, who "perform their hardest work for next to nothing, but sell the bye-products of their labours at double prices." But in spite of the mistakes, Swammerdam's account of *Sepia* was a very important contribution to the anatomy of the Cephalopods, and it is only fair to him to mention that his account of *Sepia* was based on investigations of two male specimens, and short notes taken in great haste during the four days

he spent on the dissection. For his account of the female organs he had only some old drawings with very brief notes. Considering this, the amount he accomplished was remarkable.

The most striking of Swammerdam's mistakes was his failure to discover the ducts from the liver to the caecum. He says that "the whole of it is enclosed in a special membrane, and does not have any resemblance to a liver. But I would not deny that it may perform the functions of a liver, since nature is infinite in her marvels, and God, the Author of nature, in His great wisdom, has formed different parts in different animals for the same purpose, as is most clearly seen in the marvellous construction of the genital organs, which are more conspicuous in their cunning and beauty than any words can describe."

Of these latter organs, which he confused with the renal and pancreatic appendages, he later writes "so it is enough for me to have shown the construction of these parts to be beyond measure beautiful and cunning, to the eternal glory of the omnipotent Architect, while I have no hesitation in confessing my ignorance about the remainder."

Hunter in a paper published in 1782 referred for the first time to the presence of an "organ of hearing" in Cephalopods, but this reference was not accompanied by any description. The numerous preparations he made of *Sepia*, which are still preserved in the museum of the Royal College of Surgeons, attest his extensive knowledge of this animal. His dissection of the main trunks of the circulatory system shows that he clearly understood the relationships of the branchial and systemic hearts, and his dissections of the digestive system show his understanding of the relationship between the liver and the spiral caecum. Unfortunately Hunter's work has never been published in full, and even where descriptions are not entirely lacking, they are all too brief.

The first description of the statocysts was given by Scarpa (1789).

Owing to the great similarity of structure found among the Cephalopoda, anatomical discoveries in one species frequently meant an advance in the knowledge of the anatomy of the whole Class. Thus Monro in 1785 in his anatomy of *Sepia loligo* (*Loligo sagittata*) published the first accurate account of the three hearts of Dibranchiates, though his description of the reproductive and renal systems was not correct.

The foundations of the general anatomy of the dibranchiate Cephalopods were completed by Cuvier (1817), in his "Mémoires pour servir à l'histoire et à l'Anatomie des Mollusques," which included a description of the anatomy of *Sepia*. Cuvier was acquainted with all the important literature on the Cephalopods published up to this date, and corrected the outstanding mistakes of previous authors. By now, the general anatomy of the Cephalopoda was understood well enough to enable zoologists to concentrate on particular systems, and in many important works *Sepia officinalis* has been one of the chief types studied.

Outstanding among the many more recent publications which have a bearing on the anatomy or physiology of *Sepia* are the works of Voltz (1830 and 1840) on the homologies of the shell, Chéron (1866) on the nervous system, Vigelius (1880) on the coelom and the renal sac, Grenacher (1886) on the retina, Pelseneer (1888) on the morphology of the arms, Appellöf (1893) on the finer structure of the shell, Krause (1895) on the poisonous nature of the salivary glands, Steinach (1901) on the mechanism of the chromatophores, Hamlyn-Harris (1903) on the statocysts, Cuénot (1907) on the functions of the liver, Naef (1921) on affinities among the Cephalopoda, and Alexandrowicz (1927) on the accommodation of the

eye. These are, however, only a selection from a long list of important works.

But even now, while our knowledge of the anatomy of *Sepia* is fairly complete, there is still much uncertainty in the field of physiology.

EXTERNAL CHARACTERS*.

As already mentioned (page 9), the physiological, as opposed to the morphological orientation will be used, as this avoids a great deal of confusion, and is the orientation usually adopted in the study of Cephalopods, though the older authors used the morphological.

Figure 1 represents a lateral view of the cuttlefish in its normal swimming position. From this figure and from Figures 3 and 4 which represent ventral and dorsal views respectively, of a preserved male specimen, some idea of the animal's form can be gained. It is plump, dorso-ventrally compressed, and bilaterally symmetrical. A large specimen has an overall length of about 18 inches, measured to the tip of the arms, but preservation causes a certain amount of contraction.

There is a prominent head which bears a pair of large highly developed eyes, and 10 circumoral appendages, differentiated into four pairs of arms and one pair of tentacles. Figure 7 shows an anterior view of the mouth and arms of a female specimen. The arms have been extended radially to display the mouth region. The mouth is surrounded by a circular papillated lip (I.L.). Two very powerful horny jaws, the ventral overlapping the dorsal, can be seen within the mouth opening. The mouth region consists of a bulbous oval mass (Fig. 36, B.M.), composed mainly of the large jaw muscles, called the

* To obtain a general idea of the anatomy of *Sepia officinalis* plates I and XXIV should be studied.

buccal mass, which lies within a cavity enclosed by the united bases of the arms. It is attached to the surrounding tissues on the outside only by a fold of skin, continuous with the outer lip (Fig. 7, O.L.). This allows the whole buccal mass some degree of freedom, so that it can be extended, retracted and even rotated (by the action of the muscles to be described later), to facilitate the working of the jaws.

Surrounding the outer lip is a fold of tissue called the buccal funnel (B.F.). This structure contracts greatly on preservation so that it is usually much distorted. It is attached to the bases of the eight arms at seven places by radial folds, the attachments to the dorsal pair of arms having fused together. These radial folds which support the buccal funnel are called the buccal pillars. In life the buccal funnel can be opened or closed over the mouth so that it completely covers the latter, and in the female the ventral part of the buccal funnel is modified to form a bursa copulatrix (B.C.) or depository for the spermatophores. This takes the form of a hollow on the inner side in which the spermatophores are placed by the male during copulation, and old spermatophores may often be found adhering there in a mature female. The base of the ventral side of the buccal funnel is thickened to form a sort of pad, probably to prevent the buccal mass from pressing against the bursa.

The arms (Fig. 3, A 1-4.) are numbered 1 to 4 on each side, the dorsal pair being number 1 and the ventral pair 4. The bases of all but the ventral pair of arms are connected by interbrachial webbing (Fig. 7, I.W.). Three buccal pockets (B.P.) are formed on each side, at the bases of the arms 1, 2 and 3, and 3 and 4, bounded by the interbrachial webbing, and the buccal funnel and pillars. The arms are tapering and highly muscular. On their oral surface they each bear four longitudinal rows of stalked suckers.

The sucker-bearing surface is bounded on either side by a delicate margin. In life these two margins are normally held so that they almost completely cover the suckers. The fourth pair of arms have a prominent lateral ridge towards the base, very conspicuous when the animal is swimming, but usually somewhat contracted in preserved specimens. In the male, the proximal half of the fourth arm on the left side is modified (Fig. 12). The suckers are greatly reduced, except at the base of the sucker-bearing surface where there are a few normal ones. In addition, part of the surface where the suckers are reduced appears to be glandular (M.S.). The suckers on part of the ventral arm on the right side are also sometimes slightly reduced, while those on arms number 3 show in the details of their structure a higher degree of development than the average. The modifications of one or more of the arms in the male is called hectocotylisation, and the arm or arms affected are said to be hectocotylised. In some Cephalopods these modifications, which are associated with copulation, are quite remarkable.

The tentacles (Figs. 7, 11.) each of which consists of an expanded sucker-bearing head at the end of a long stalk, originate from within pockets lying between the third and fourth arms. These pockets are large and extend right back to the posterior limit of the head, immediately ventral to the eyes (Fig. 25, T.PO.). In life the tentacles are normally coiled within the pockets except for their sucker-bearing ends. In dead specimens, however, they are usually extended. The tentacle head has a prominent swimming margin (Fig. 11. S.M.) and delicate margins to the sucker-bearing surface (D.T. and V.T.). At the apex of the tentacle is a curious little terminal pad (T.P.). The suckers, which are arranged more or less in longitudinal rows, vary immensely in size. The central row includes several very large ones, with smaller ones on either side.

The eyes (Fig. 1, unlettered) which project slightly dorso-laterally, lie within their orbital chambers, completely covered by the skin. Opposite the pupil this is modified to form a crescent-shaped transparent window or cornea (Fig. 4, COR.) through which the dorsal flap of the iris (IR.) can be seen. There is a simple ventral eyelid (EL.) which can be drawn over the cornea. Under the eyelid, where it joins the cornea at the anterior end, the tiny pore of a short passage communicating with the orbital chamber (Fig. 59, D.O.) can be seen with the aid of a lens.

A short way behind each eye there is a small ciliated pit (Fig. 1, O.P.) usually termed the olfactory pit. The position of these pits just in front of where the water of respiration enters the mantle cavity seems to indicate that their function is that of osphradia.

On the ventral side of the head lies the large aperture of the exhalent tube of the funnel (Fig. 3, F.). The funnel almost completely encircles the neck. It is a very muscular organ, attached on the dorsal side to the crescent-shaped nuchal cartilage (Fig. 24, N.C.). It consists of two parts, a ventral exhalent tube (E.S.F.), and a pair of lateral pockets (L.P.). A pair of cartilaginous projections on the inside of the mantle (M.C.) lock into corresponding depressions (F.C.) on the posterior ventral surface of the funnel. The structure and function of the funnel will be described in greater detail later (pages 25, 29, 55, 98).

The rest of the body or trunk is composed of the shield-shaped mantle (Figs. 3, 4.) enclosing on the ventral side a large mantle cavity (Fig. 5, M.CA.) which contains the viscera. On the ventral side the mantle consists of a thick muscular wall (Figs. 3, 81, M.M.). On the dorsal surface the hard shell lies just beneath the tough integument which covers it. Anteriorly the mantle cavity opens to the exterior all round the head, which is attached to the rest of the body on the dorsal side about an inch and a half

within. On this side the anterior mantle margin projects forward somewhat, outlining the shape of the anterior end of the shell. The ventral surface of this projection is lined by the dorsal cartilage (Fig. 24, DO.CA.), which fits against the nuchal cartilage. On either side of the mantle a well-developed swimming fin (Fig. 4, FI.) is attached. The fins commence about half an inch from the anterior margin of the mantle and extend to the extreme posterior end, where they are separated only by a groove.

The skin of the cuttlefish, as of all dibranchiate Cephalopods, is remarkable because of the extraordinary colour effects and changes of which it is capable. These are brought about by chromatophores and iridocytes which lie in the dermis (see APPENDIX E, page 151, for practical details of preparation of chromatophores). Figures 8 and 9 show a diagrammatic section and surface view respectively of the skin from the back of *Sepia officinalis* under the microscope, while Figure 10 shows a single chromatophore in surface view, (*a*) contracted, and (*b*) expanded.

Each chromatophore consists of a little flattened elastic nucleated pigment sac, from which radiates contractile fibres (Fig. 10, M.CR.). At the base of each bundle of fibres there is a nucleus (N.M.CR.). The fibres have their moveable ends attached to the sac, their other ends being fixed in the skin. The expanded state is the active one, and is brought about by the contraction of the elastic fibres. Retraction of the expanded chromatophore is brought about by the elasticity of the chromatophore sac. Steinach (1901) finally established the muscular nature of the fibres of the chromatophores, after many years of controversy. The chromatophores are of three kinds; dark ones, varying in colour from sepia to a more or less reddish colour, yellowish-brown and orange. The iridocytes (Figs. 8, 9, I.) consist of cells having a fine

reticulate structure which defracts the light giving a yellowish-green and reddish iridescence. The iridocytes lie beneath the chromatophores. Colour changes are controlled by the central nervous system.

The chromatophores are very much more numerous on the dorsal than on the ventral side of the body. The normal colouration of the cuttlefish is not conspicuous. In life it is usually either a uniform brownish grey, or motley, while sometimes the back and dorsal surface of the lateral ridges of the ventral arms show light transverse dichotomising stripes on a darker background, according to the nature of the surroundings. The ventral surface of the body is much paler than the dorsal. The male is characterised by a white line which runs along the dorsal surface of the edge of the fins. For several hours after death fluctuations of colour continue, and can be induced by artificial stimulation. Preserved specimens do not usually retain their natural colour.

MANTLE CAVITY.

[DISSECTION.—*To expose the mantle cavity make a median longitudinal cut through the mantle wall from the anterior margin to the posterior end, passing a little to one side of the median septum which divides the posterior part of the mantle cavity into two parts. Open the funnel by a median longitudinal cut. It is advisable to inject the veins and arteries, as the former especially, owing to their very thin walls, are difficult to recognise, in spite of their very large size. For practical instructions concerning injection see Appendix D, page* 149.]

A. Male.

Figure 5 shows the mantle cavity of a male specimen. The ventral side of the mantle consists of a thick muscular wall (C.M.). On its inner side towards the anterior end are

a pair of projecting knobs, each supported by a cartilaginous core, called the mantle cartilages (M.C.), which fit into corresponding cartilaginous depressions, called the funnel cartilages (F.C.) situated on the posterior surface of the ventral side of the funnel. These form part of a locking mechanism which prevents exhalent water from escaping from the opening of the mantle cavity round the funnel. The rest of this mechanism consists of the nuchal cartilage (Fig. 79, N.C.) on the dorsal surface of the neck, which fits against the dorsal cartilage (DO.CA.) on the ventral surface of the dorsal part of the mantle cavity. The sides of the mouth of the mantle cavity which represent the inhalent channels (Fig. 24, I.SI.) are effectively blocked to exhalent water by the lateral pockets of the funnel (Figs. 5, 24, L.P.) which are distended by the pressure of the water trying to escape. Thus exhalent water has to pass out through the central tube of the funnel (Fig. 24, E.S.F.).

The posterior part of the mantle cavity is divided into two chambers by an elastic membrane stretching from the ventral to the dorsal side. This membrane also forms the posterior limit of the mantle cavity about 2 inches form the posterior apex of the mantle. A small median mantle artery and vein (Fig. 5, M.A.V.) run up the anterior edge of this septum, and then travel anteriorly along the inner surface of the mantle for some way before penetrating deeper.

The bulk of the mantle cavity is occupied by the visceral dome. This is covered by a thin but tough membrane, through which parts of the anatomy can be made out without dissection. As these form indispensable guides to the actual dissection they are included in the description of the mantle cavity. The anterior part of the visceral dome contains the large paired digestive glands (L.), often referred to as the liver, which are enclosed within a muscular capsule, lying within the sheath formed

by the retractor muscles of the head (R.H.). Lateral to the latter lie the large retractor muscles of the funnel (R.FU.), which extend posteriorly to the base of the branchiae (B.). Each branchia is fastened to the mantle wall along most of its length by a thin membrane terminated anteriorly by a strong ligament (B.L.). The framework of the branchia is formed by the retractor muscle (Fig. 5, M.R.B., Fig. 25, M.R.B. and A.R.B.), of which, however, only the ventral part can be seen in Figure 5.

[DISSECTION.—*Continued from page 24. Before examining the rest of the mantle cavity, sever the median septum so that the mantle wall can be folded completely to the sides. Starting at the posterior end and* ***taking great care not to damage the inksac*** (Fig. 5, IS.), *remove the skin from the posterior part of the visceral dome up to just behind the renal papillae* (RE.P.). *If this is done properly a very thin membrane should still entirely cover the visceral dome. The outer skin, which is continuous with the mantle epithelium, comes away from this underlying membrane fairly easily.* ***Owing to the extreme delicacy of this membrane and of the other membranes which limit the coelomic and renal chambers, further examination and dissection should always be carried out under water.***]

The rectum (Fig. 5, RE.) lies along the middle line, loosely attached along its dorsal edge to the capsule enclosing the digestive glands by means of a median adductor muscle (Fig. 23, A.RE.), whose origin is on the anterior part of the ventral surface of the capsule of the digestive gland. The anus (Fig. 5, AN.) is bounded by four lips, a small dorso-ventral pair, and a leaf-like lateral pair (Fig. 43, AN.V.). The inksac (Fig. 5, IS.) can be recognised by its metallic colour. Continuous with the inksac is the inksac duct which runs forward and enters the rectum on the dorsal side just behind the anus.

Anterior to the rectum the large median cephalic vein (CE.V.) runs along the ventral surface of the capsule enclosing the digestive gland. Anteriorly it is covered by the funnel, while posteriorly it runs just dorsal to the rectum, covered by the retractor muscle of the rectum, and forks in the region of the renal papillae (RE.P.) into two venae cavae. Two pairs of factors enter the cephalic vein along that part of it which is visible. The first of these, which returns blood from the funnel and from the retractor muscles of the head can be seen when the funnel is opened (Fig. 6, P.F.V.) ; the other pair (Fig. 5, P.V.R.M.) returns blood from the posterior part of the head and funnel retractor muscles, and enters just by the renal papillae.

On either side of the rectum extends the renal sac (RE.S.) which opens into the mantle cavity by the paired papillae previously mentioned. Through the walls of this sac can be seen the renal appendages which hang from the walls of the veins which lie within it. The posterior mantle veins (P.M.V.) enter the renal sac from the posterior part of the mantle wall by sinus-like expansions. Just before the posterior mantle vein on the left side enters the renal sac, a small vein from the genital duct enters it on the anterior side, and the siphuncle vein (Fig. 6, S.V.) from the posterior apex of the mantle. These veins are not lettered in Figure 5. Lateral to the base of the branchiae similar expansions of the anterior mantle veins (Fig. 5, A.M.V.) can also be seen. The outline of the branchial hearts (B.H.), to which are attached the pericardial glands (P.GL.), show through the pericardial membrane which encloses them, just posterior to the bases of the branchiae.

The posterior aorta (P.AO.) comes to the surface on the left side of the ink duct where the latter merges from the ink sac. It divides into paired posterior mantle arteries (P.M.A.) which pass ventral to the inksac and enter the

mantle wall. Another small artery, the vestigial siphuncle artery (Fig. 6, S.A.), partly obscured in Figure 5 by the elastic membrane covering the posterior part of the visceral dome, runs over the ventral surface of the inksac posteriorly towards the region of the siphuncle.

The male genital duct (Fig. 5, M.D.) emerges from the visceral dome near the base of the left branchia and projects within the mantle cavity. This is part of Needham's pocket, which forms a reservoir for spermatophores. It is attached by a membrane and a ligament continuous with the retractor muscle of the rectum. About one-third of its length from its emergence from the visceral dome it bears on the lateral side a tiny aperture (Figs. 5, 74, A.G.S.), which is easily visible to the naked eye if its exact position is known. This is the external aperture of the genital sac (Fig. 74, G.S.) in which the apparatus which makes the spermatophores is enclosed.

Parts of the nervous system can also be seen without dissection. The very large paired stellate ganglia (Fig. 5, S.G.) lie on the mantle wall just by where the neck attaches to the trunk. Numerous nerves radiating from them can be seen showing through the skin which lines the mantle cavity. The paired visceral nerves (V.N.) run along the sides of the cephalic vein during most of that part of its course which is visible. Shortly after they emerge to the surface each gives off a branch (Fig. 6, N.R.F.) to the retractor muscle of the funnel. If the visceral nerves are followed posteriorly large branches can be seen forking outwards and backwards in the region of the renal papillae. These run along the anterior margin of the renal sac to the bases of the branchiae, where they are expanded into comparatively large branchial ganglia (Fig. 54, B.GA.). These ganglia can be seen if the bases of the branchiae are turned outwards and backwards.

B. Female.

[DISSECTION.—*This is the same as for the male, except that when the posterior part of the visceral dome is skinned, the nidamental and accessory nidamental glands should be removed. In the case of ripe female specimens, the eggs with which the posterior part of the coelomic cavity is packed swell up so much after the specimen has been in water for a short time as to make satisfactory dissection of that part impossible. Females caught after spawning are best for dissection.*]

Figure 6 shows the mantle cavity of a female specimen. It differs from the male only in so far as the female genital duct has a large gland (Fig. 72, G.OD. and Fig. 6, unlettered) attached to it, and the posterior part of the visceral dome is obscured by two pairs of glands. The larger pair, the nidamental glands (Fig. 6, N.) are ovoid in shape, and have apertures at their anterior ends. The other pair, lying anterior to the nidamental glands are called the accessory nidamental glands (AC.N.G.). These are orange-coloured and of rather intricate shape. They open to the exterior by numerous minute pores (A.A.N.G.) which can be seen in a fresh specimen by placing it under water, and gently pressing the glands, when some of their contents exudes.

Apart from the presence of these glands, and the small arteries, veins and nerves which supply them, the anatomy of the female mantle cavity is identical with that of the male, though the exact proportions of male and female specimens show marked differences.

INSIDE OF FUNNEL.

Figure 6 shows the exhalent tube of the funnel opened. Three glandular patches (F.G.), one median and two lateral, are attached to its dorsal surface. These are called the organs of Verrill. In preserved specimens these

glands are inclined to disintegrate after a time, so that they are scarcely recognisable. Towards the anterior end of the funnel there is a valve (F.V.) which prevents water from entering the mantle cavity through the exhalent tube of the funnel.

COELOMIC CAVITIES.

The coelomic cavities consist of the viscero-pericardial coelom and the renal sac. According to the work of Naef (1909) on *Loligo*, both these cavities develop in a rather similar way from splits in mesodermic anlagen. Subsequently their lumina become continuous, and the epithelium which lines them is also continuous. This work contradicts the statement of Faussek (1901) that no primary connection exists between the renal sac and the pericardium.

The first accurate description of these cavities in Sepia was given by Vigelius (1880). The renal sac consists of three chambers, two of them ventral and symmetrically placed on either side of the rectum just under the skin which covers the visceral dome on the ventral side, while the third is median and dorsal. These three chambers communicate by a large lumen at their anterior end, and so they constitute a single renal sac.

The viscero-pericardial coelom (Figs. 22, 79, VP.) is a large bag-like cavity, which, as the name implies, contains the hearts, some of the viscera, and also the gonad. It extends nearly to the posterior end of the visceral dome, and its anterior part is sandwiched between the dorsal (Figs. 22, 79, D.C.) and ventral (Figs. 20, 79, V.CH.) chambers of the renal sac. It divides anteriorly into two funnel-shaped portions which open into the renal sac by small apertures (Figs. 20, 22, A.VP.C.) at the bases of the renal papillae.

[DISSECTION.—Continued from page 26. *Free the inksac from the walls of the visceral dome, starting at the posterior end and working forwards.* ***Take care not to puncture it, or the ink it contains will obscure the dissection.*** *It is necessary to free the right posterior mantle artery* (Fig. 20, P.M.A.) *from the ventral wall of the inksac. Cut through the inksac artery and vein* (IS.A. and IS.V.), *which enter the inksac about the middle of its dorsal surface, and then detach all but the most anterior part of the ink duct from the visceral dome and rectum, so that it can be placed out of the way as shown in Figure* 20. *Open the ventral renal chambers* (V.CH.) *by slitting open the renal papillae* (RE.P.) *and continuing backwards.* ***Take care not to damage the apertures of the viscero-pericardial coelom*** (A.VP.C.) ***when doing this.*** *Open the capsules in which lie the branchial hearts* (B.H.). *Cut windows through the posterior part of the viscero-pericardial coelom* (VP.) *and the posterior part of the dorsal renal sac* (C.D.C.) *as shown in Figure* 20. *The extent of the body cavities can now be investigated almost completely with the aid of a seeker, but owing to the thinness of the limiting walls, great care should be taken not to tear them.*]

A. Ventral Chambers of Renal Sac.

Figure 20 represents a dissection of the ventral renal chambers. They are filled with flocculent appendages of the veins which lie within them, most of which however, are represented as having been clipped away in the figure. These two chambers, as already mentioned, are symmetrically placed on either side of the rectum, and are separated from the mantle cavity on the ventral side only by the comparatively tough skin which covers the ventral wall of the visceral dome, and by their own delicate wall which lies immediately under the skin. They open into the mantle cavity by paired renal papillae (RE.P.), situated at the anterior end of the chamber on either side of the rectum, which are closed by sphincter muscles. Anteriorly the left and right ventral chambers

communicate with one another via the anterior part of the dorsal chamber. The left ventral chamber communicates with the dorsal chamber by a large lumen (L.V.D.) situated at the anterior end of this chamber. Within this lumen can be seen the flocculent appendages of the ducts of the digestive glands, which are easily confused with the appendages of the veins lying in the ventral chambers, unless the veins have been injected, when the appendages of the latter are coloured by the injection. The right ventral chamber communicates with the median dorsal chamber by a large opening extending lengthwise from its anterior end to the mid-point of the intestine loop (Fig. 22, LI.V.D.), and dorsal to the rectum. Posteriorly the ventral renal chambers communicate directly by a small passage (Fig. 21, C.V.C. and Fig. 20, not lettered) immediately posterior to the intestine loop. This passage is bounded by the posterior aorta on its dorsal side, and the ink gland artery ventrally. The latter is given off from the posterior aorta immediately after it leaves the ventricle, and travels at first slightly anteriorly before running posteriorly, and from it is given off a small artery to the intestinal loop. The general extent of the ventral renal chambers will be seen from Figure 20. Dorsally they are separated from the anterior part of the viscero-pericardial coelom only by a very thin membrane, and the outline of the funnel-shaped cavities of the anterior part of the coelom, which lead to its apertures (Fig. 20, A.VP.C.) into the renal sac, can be seen showing through.

Large paired venae cavae (V.C.) formed by the forking of the cephalic vein (CE.V.) pass through the ventral renal chambers. These veins receive paired posterior and anterior mantle veins (A.M.V. and P.M.V.), and in addition each receives a mesenteric vein (R.M.V. and L.M.V.). The right vena cava also receives the large inksac vein (IS.V.) and two small factors from the walls of the ventricle,

while the left vena cava receives a small factor from the loop of the intestine (Fig. 20, unlettered). All the veins which run through the ventral renal chambers are attached to the dorsal walls of the chambers, while the sides which lie freely in the chambers are covered with the venous appendages already referred to.

B. Viscero-pericardial Coelom.

[DISSECTION.—Continued from page 31. *Remove the veins with their appendages from the ventral renal chamber, and then cut through the ventral wall of the viscero-pericardial coelom longitudinally from the posterior end, continuing the cut on either side of the posterior aorta. This involves severing both the posterior mantle arteries. The ventral walls of the viscero-pericardial coelom can now be turned to the sides.*]

Figure 21 represents diagrammatically a dissection of the viscero-pericardial coelom, and the dorsal chamber of the renal sac. Figure 22 shows the outline of the viscero-pericardial coelom and renal sac. The description should be referred to when these figures are studied.

As mentioned above the viscero-pericardial coelom is a large bag-like cavity (Fig. 22, VP.), the anterior part of which lies between the dorsal and ventral chambers of the renal sac. Anteriorly it divides into two symmetrically placed funnel-like parts which open by small apertures (Figs. 20, 21, 22, A.VP.C.) into the ventral renal chambers (Fig. 20, V.CH.) just posterior to the renal papillae (RE.P.).

About half way from these apertures to its posterior limit there is a transverse flap (Figs. 21, 22, T.VP.) attached to its ventral wall, and extending across the entire width of the coelom. In the middle line where it crosses the dorsal wall of the posterior aorta, this flap is very narrow, but on either side it broadens to form the dorsal walls of symmetrically placed pockets (P.B.H.), which open

anteriorly into the main cavity of the coelom, and contain the branchial hearts. On the left side the dorsal boundary of the coelom is formed by the thin transparent membrane which separates it from the dorsal renal chamber, and through this wall can be seen the spiral caecum (Fig. 21, CA.) and the appendages (PA.) which cover the ducts (D.L.) of the digestive glands.

Occupying most of the anterior part of the coelom is the ventricle (VE.), which is situated somewhat on the right side. It is a stout muscular organ, and is bent upon itself at approximately a right angle, one arm of which points anteriorly and leads into the cephalic artery, while the other points transversely towards the left side where it receives the left auricle. The entrance of the right auricle (AU.) is shown in the Figure. The ventricle lies quite freely in the viscero-pericardial coelom except in the region where the cephalic artery is given off at the anterior end, where the posterior aorta is given off and where veins from its walls, which pass into the right vena cava leave it. At these points it is attached to the coelomic wall. The auricles are attached to the ventral coelomic walls except for a short distance before they enter the ventricle.

The branchial hearts are attached to the walls of the pouches in which they lie in two places; anteriorly where the afferent branchial vessels are given off, and on that part of their surface which faces inwards and forwards. Attached to each branchial heart is the pericardial gland.

Most of the right side of the coelom is occupied by a large stomach (Fig. 21, ST.). Only part of the stomach however, lies within the coelom, for the wall of the dorsal renal chamber runs from the dorsal wall of the visceral dome to the dorsal wall of the stomach, roughly along the longitudinal middle line of the latter, so that the left hand part of the dorsal surface of the stomach lies in the dorsal renal chamber. The posterior part of the coelom is

occupied by the gonad. Both ovary and testis (TE.) open into the coelom, and in both sexes the genital duct (Fig. 22, GD.) opens from the ventral wall of the coelom, slightly on the left side, and towards the posterior end. Thus the genital duct is a continuation of the coelomic cavity.

If the ventricle is lifted forwards the course of the right genito-mesenteric vein and the genital artery (Fig. 21, G.A.V.) can be followed. Both run close together straight backwards, near the left side of the stomach. They lie in the mesentery which separates the left side of the dorsal renal chamber from the coelom and which is attached to the stomach along this side. The genito-mesenteric vein receives large factors from the stomach, caecum, and appendages of the duct of the right digestive gland. Thus it fulfils the functions both of right mesenteric vein and genital vein, and it is for this reason that I have called it genito-mesenteric. Earlier authors were divided between the terms "genital" and "right mesenteric." The genital artery runs straight from the heart, from the angle of which it emerges on the anterior side, to the gonad, giving off only a few very small branches to the mesentery.

C. Median Dorsal Chamber of Renal Sac.

[DISSECTION.—Continued from page 33. *Cut through the thin membrane on the left side which separates the viscero-pericardial coelom from the ventral wall of the dorsal renal chamber, starting at the posterior end and continuing forwards to the lumen communicating between the ventral and dorsal chambers of the renal sac. In doing this the left auricle will be cut through. Detach the rectum from the visceral dome, starting at the anus and working back as far as the intestinal loop. Cut through the cephalic vein just anterior to where it forks into the two venae cavae.*]

In Figure 21 the membrane separating the ventral wall of the dorsal renal chamber from the coelom has been cut away. In this chamber lie the two large ducts (D.L.) already mentioned, leading from the paired digestive glands, often called the liver (Fig. 36, L.), which occupy all the anterior part of the visceral dome, to the caecum. These ducts enter the anterior extremity of the dorsal renal chamber close to the middle line, and here they are attached to the oesophagus which also enters at this point. They run straight back, passing on either side of the intestine, and unite just before they enter the spiral caecum (Fig. 21, CA.) on its ventral side. These ducts are festooned with voluminous hollow glandular appendages (PA.), usually called the pancreas, which open into the ducts of the digestive glands by large orifices. These appendages obscure the ducts themselves from view. The ducts of the digestive glands do not lie freely in the cavity of the renal chamber, but are attached to the oesophagus during the anterior part of their course, and then to the intestine, by a mesentery along one edge.

The posterior part of the left side of the dorsal renal chamber is occupied by the spiral caecum (CA.), which is only attached to the membrane enclosing the chamber where it communicates with the stomach. Leaving the caecum on the anterior side, and close to where the stomach opens into it, is the intestine (IN.). This is attached by a mesentery to the wall of the chamber throughout its course, and passes through the ventral wall of the chamber a little before it loops. The right side of the chamber is bounded ventrally by the dorsal wall of the stomach.

The left mesenteric vein runs close to the duct of the left digestive gland. This large vein receives numerous factors from the left pancreas, and also from the intestine and spiral caecum.

From the left side of the trunk of the cephalic artery, just after it emerges from the heart, the ventral gastric artery (Fig. 47, V.G.A.) is given off. This supplies the ventral side of the stomach, the intestine, the caecum and parts of the left and right pancreas. Immediately after emerging from the cephalic artery it gives off two additional branches. One of these, the anterior genital artery (A.G.A.) runs first forwards in the walls of the renal sac, a little on the right side of the oesophagus, up to the extreme anterior end of the renal sac, where it crosses the oesophagus ventrally, and continues in the wall of the renal sac to the anterior part of the genital duct. The other, the posterior oesophageal artery (P.O.A.), is quite small, and runs on the dorsal side of the oesophagus anteriorly. It can only be seen after a little dissection.

The full extent of the median dorsal chamber of the renal sac can best be seen by removing the shell, and opening up the cavity from the dorsal side.

[DISSECTION.—Continued from page 35. *Cut through the skin of the back from the apex of the mantle to the extreme posterior end. Fold back the skin on either side, exposing the surface of the shell. Cut through the muscle, which, in addition to the skin, helps to form the shell capsule at the posterior end. Remove the shell by displacing it anteriorly. Remove the loose connective tissue which lies between the thin ventral wall of the shell capsule and the dorsal wall of the renal sac, and then open the latter by a longitudinal cut.*]

When the dorsal renal chamber is opened from the dorsal side, the caecum can be pulled right out of the chamber, and its attachment to the stomach more clearly seen than when it is viewed from the ventral side. The posterior part of the oesophagus can also be seen where it emerges from between the paired digestive glands and enters the stomach. The very large trunk of the cephalic

artery, after leaving the ventricle, passes round to the dorsal side of the oesophagus, to which it is fastened, and then goes through the anterior wall of the renal chamber. This cephalic trunk gives off the dorsal gastric artery (Fig. 47, D.G.A.) from its left side. This artery can be clearly seen without further dissection. It supplies the dorsal surface of the stomach, and part of the left pancreas.

SKELETON.

Sepia possesses a highly developed skeleton, which serves to increase the animal's rigidity, and so to increase the efficiency of the muscular system. This skeleton consists of two parts, viz., the shell and the cartilaginous skeleton.

It is difficult when describing the anatomy of a member of the most highly organised of all the invertebrate Classes, to avoid analogies with the Vertebrates. Although cephalopod anatomy is profoundly different from that of any Vertebrate, yet it is possible to say that the shell serves the animal as a backbone, and the cephalic cartilage as a skull. It would be unwise however, to attempt analogies with regard to the other parts of the cartilaginous skeleton.

A. Shell.

The shell lies within the shell sac, and is secreted by the epithelium which lines it. Unlike the analogous vertebrate structure it is entirely dead, and is composed of calcareous and horny matter. The main muscles of the trunk and neck encircle its horny margin, but unlike the muscles which have their origin on the cartilaginous parts of the skeleton, no muscles are actually attached to the shell. In addition to giving rigidity to the trunk, the shell, owing to its lightness, plays an important part in the equilibrium of the animal. Not only does it materially

alter the specific gravity of the animal as a whole, but owing to its position close to the dorsal surface, it must greatly assist in maintaining the normal swimming poise shown in Figure 1.

Krause (1830 and 1840) first established the homologies between the sepia shell and those of *Nautilus*, *Spirula* and the Belemnites. The modern cuttlefishes made their appearance in the Miocene period, and were undoubtedly derived from a Belemnite ancestor called *Beliosepia*, which lived in the Eocene seas, and is found in a fossil state in the London clay.

The evolutionary process has been one of constructive development of certain parts of the more primitive shell combined with reduction of others. To understand the shell of *Sepia* it is therefore necessary to review the stages through which the primitive Cephalopod shell has passed in the course of evolution. If we accept that the Mollusca are a homogeneous group, then the primitive cephalopod shell was a simple limpet-like cone. Unknown forces dictated that development should proceed along the lines of the secretion of septa, with the resultant transference of the animal away from the apex.

The following account of the further evolutionary stages in the development of the sepia shell is taken from the work of Naef (1921). The work is based on the systematic study of the fossil and recent Cephalopods, supplemented by embryological studies. Text figure 4, *a-d* shows four diagrams which represent links between the modern cuttlebone and the primitive cephalopod shell. The latter (Text figure 4*a*) consisted of a simple cone called the phragmocone, the apex of which was partitioned off (C.PH.) by transverse septa, perforated by a central tube called the siphuncle (SI.). The animal inhabited only the last chamber of the cell (L.CH.). From this primitive shell two divergent courses of evolution proceeded: (1) the

coiling of the long and increasingly unwieldy shell, which took place in the Ammonites, a process analogous to that followed by the Gastropods, and adapted to sedentary habits; (2) evolution associated with the acquisition of an active swimming habit, in which the terminal shell, so essential to a sedentary habit as a protection, became only an encumberance. It was along these lines that the evolution of the Decapoda proceeded.

Text figure 4*b* shows the second stage. The shell has been completely enclosed within the mantle, through the latter growing back over it from the anterior end of the shell, and the rather delicate phragmocone is encased in a new structure, the guard or rostrum (RO.), which is continued forward on the dorsal side as the proostracum or pen (PR.). The ventral half of the phragmocone is reduced, so that the siphuncle is no longer quite central, and the ventral wall of the terminal living chamber of the shell has been completely replaced by the muscular mantle (M.M.).

In the next stage (Text figure 4*c*) the rostrum is highly developed while the phragmocone has become curved and concave on the ventral side, and tucked into the body. As a result of this the muscular mantle is now attached to the outside of the shell.

In the final stage (Text figure 4*d*) the rostrum, the proostracum, and the ventral part of the phragmocone are vestigial, while the dorsal part of the latter (D.PH.) which is enormously developed, is characterised by the septa being obliquely tilted.

[DISSECTION.—Sepia *shells should be kept wet, as they are very liable to crack if they are allowed to dry. To cut the shell in half longitudinally, the best method is to saw through the shell a little to one side of the middle line, and then grind down the larger portion on a fairly coarse revolving wheel. Finish on a smooth hone. To examine the septa and trabeculae of the dorsal part of the phragmocone it is better to*

break the shell than to cut it, as they show up much better when it is broken. To facilitate breaking, the hard dorsal surface can be sawn through.]

Figures 15-19 illustrate the structure of the shell of *Sepia*. The cuttlebone is a familiar object on the sea shore. Being very light it floats in the water, and on occasions these bones are brought inshore in such numbers that they have been christened " sea foam."

A very detailed description of the structure of the shell of *Sepia officinalis* was given by Appelöf (1893), illustrated by some fine plates. Only an outline of the structure is given here.

The cuttlebone of *Sepia* consists essentially of three parts :—

1. A very large calcareous phragmocone (Fig. 15, L.S., S.R. and V.PH.).

2. The shell margin (H.SH. and C.SH.), partly calcareous, and partly horny, which completely surrounds the phragmocone.

3. The vestigial calcareous rostrum (Fig. 15, RO., Fig. 17, C.RO.), also surrounded by horny material (H.RO.).

The chief interest centres round the phragmocone, which has undergone profound modification along the lines described above. The dorsal part, which may be referred to as the " pad," consists of very closely applied septa obliquely tilted from the primitive position at right angles to the axis of the shell. These septa are supported by calcareous trabeculae (Fig. 19) which in places lie in regular rows, while in others they form an intricate maze enclosing numerous minute air pockets. The dorsal part of the phragmocone is strengthened by the hard calcareous dorsal wall of the shell (Fig. 16, D.SH.). The ventral part is only recognisable as a series of striations (Fig. 17, V.PH.) which have no air spaces between them. In the middle

line these striations, each of which represents a septum, grow backwards instead of forwards, so that there is practically no ventral wall to the siphuncle. Laterally they form the "fork" (Fig. 15, F.S.).

There are slight differences in the shape of the shell in the male and female. In the latter both the fork and the posterior part of the shell margin are slightly wider than in the male.

Malacologists have distinguished three types of cuttlebone, and at one time these were classified as belonging to three distinct species, viz., *Sepia officinalis*, *S. filliouxi*, and *S. fischeri*. These three types are regarded now as three distinct varieties, but not as separate species. Although the shell of *Sepia officinalis officinalis* can be easily distinguished, the other two varieties differ only in a number of very small points, and their separation is difficult. Racially the distinction is however, very sharp (see page 142).

The cuttlebone has been used commercially for various purposes: as a dentifrice, for fine polishing, for taking casts in metal work, as an agricultural fertilizer, for pouncing and for cage birds to sharpen their beaks on.

B. **Cartilaginous Skeleton.**

This consists of the following parts:—

1. Cephalic cartilage or skull.
2. Brachial cartilage,
3. Radula cartilages,

in the head.

4. Horseshoe cartilage,
5. Sclerotic cartilage,
6. Equatorial cartilage,

associated with the eye.

7. Nuchal cartilage,
8. Dorsal cartilage,

9. Funnel cartilages,
10. Mantle cartilages,
11. Diaphragm cartilage,
12. Fin cartilages,

in the neck and trunk.

13. Branchial cartilages, which give support to the laminae of the branchiae.

1. CEPHALIC CARTILAGE.

This cartilage, which lies in the posterior part of the head, is symmetrical and of complicated form. It is in many ways analogous to the vertebrate skull. It serves three purposes: it protects the brain, which it partly encloses, from pressure by the muscles of the head; it helps to form the large and deep orbits in which the eyes are lodged; and it serves, together with the brachial cartilage, for the attachment of the powerful retractor muscles of the head, the adductor muscles of the funnel, the oculomotor muscles of the eyes, and the muscles of the arms and tentacles. It does not, however, serve the muscles of the jaws, which are quite independent of the cartilaginous skeleton.

[DISSECTION.—*Remove the skull complete with the brachial cartilage, and with the eyes still attached to the orbital and trochlear cartilages. When dissecting the muscles away, leave short lengths of the nerves which emerge through the foramina of the skull intact. Remove one eye. When this is done, the nerves which lie in the orbit can be seen without further dissection.*]

Figures 26 to 29 represent four views of the cephalic cartilage. As Figures 26, 28 and 29 have been projected from Figure 27, which is a ventral view, they are all drawn with the ventral side uppermost. As most of the dissection is done with the animal lying on its back, they appear more familiar in this position.

To simplify the description names have been given to the different regions which can be distinguished in this cartilage. The most conspicuous part consists of symmetrical lateral expansions, called the orbital cartilages (Figs. 27, 29, O.C.), which help to form the posterior part of the orbit. This part of the skull is thick and solid. Attached to the ventral edge of each of the orbital cartilages is a thin wing-like piece of cartilage, the wing of the orbital cartilage (W.O.), which also contributes to the formation of the orbit.

The two orbital cartilages are united anteriorly on the ventral side by a stout bridge (Fig. 27, BR.) of cartilage, triangular in cross-section. Posteriorly on the ventral side they are separated by the statocyst cartilage (Figs. 27, 29, SC.C.) in which lie paired statocysts, and on the dorsal side, they are connected by the cerebral cartilage (Fig. 29, CE.C.), which partly encloses the cerebral ganglion.

Projecting anteriorly and dorso-laterally from the bridge of the orbital cartilages are paired trochlear cartilages (Figs. 27, 29, TR.). These are delicate wing-like blades. Unlike the orbital cartilages, they do not form part of the orbit, but project into it, and are covered by the external argentea which attaches the eve to the orbit.

Posteriorly the cephalic cartilage is pierced by a large hole, the foramen magnum (Fig. 29, F.MA.). This is closed by a tough membrane (Fig. 26, M.P.B.) enclosing the brain posteriorly, which surrounds the peri-oesophageal blood sinus (P.O.S.) in which lie the paired buccal arteries (B.A.), the oesophagus (OES.), and the duct (D.S.G.) of the posterior salivary glands.

Two pairs of large nerves emerge through the foramen magnum. These are the visceral nerves (E.V.N.) which emerge very close together near the ventral edge of the foramen, and the pallial nerves (E.P.N.) which emerge

somewhat more laterally, together with the small posterior head retractor nerves which lie against them. The rim of the foramen magnum shows slight grooves marking the position of the emergence of these nerves.

Many of the nerves which radiate from the brain pass through the skull. Consequently in the isolated skull corresponding foramina can be seen. These foramina consist of 14 pairs, in addition to the foramen magnum, including two pairs through which only blood vessels pass. Four pairs occur in the orbits :—

1. Foramen of optic nerve.

This is the largest, but is not complete, as it is bounded on the anterior side by a stout ligament (Fig. 28, L.F.O.) which takes the place of cartilage. In addition to the very stout optic nerve (OP.N.) there emerge through this foramen three small nerves, the olfactory nerve (O.N.), the posterior oculomotor nerve (P.O.M.N.) and the superior anterior ophthalmic nerve (S.A.O.N.).

2. Foramen of superior posterior ophthalmic nerve. (Fig. 28, F.S.P.).

This is situated on the postero-dorsal surface of the orbit.

3. Foramen of inferior posterior ophthalmic nerve. (Fig. 28, F.I.P.).

This is situated a little ventral and posterior to the posterior oculomotor nerve.

4. Foramen of anterior oculomotor nerve. (Fig. 28, F.A.O.).

This is situated a little way dorsal to the base of the trochlear cartilage.

One pair occurs on the wings of the orbital cartilages.

5. Foramen of olfactory nerve. (Fig. 27, F.O.N.).

This is the foramen through which the olfactory nerve, after travelling in the orbit, passes from it to the outside.

Two pairs occur on the ventral side of the statocyst cartilage (excluding the foramina of blood vessels to be mentioned separately).

6. Foramen of anterior funnel nerve (Fig. 27, F.A.F.).

This is a large foramen, through which passes, in addition to the anterior funnel nerve, the anterior funnel artery. The foramen of the inferior posterior ophthalmic nerve (Fig. 28, F.I.P.) communicates with this foramen, as the latter nerve emerges from the brain with the anterior funnel nerve.

7. Foramen of posterior funnel nerve. (Figs. 26, 27, F.P.F.).

This foramen is postero-lateral in position.

One pair occurs in the cerebral cartilage.

8. Foramen of post-orbital nerve. (Fig. 26, F.P.N.).

This is situated postero-dorsally.

Two pairs occur on the posterior surface of the cephalic cartilage, close to the foramen magnum.

9. Foramen of collar nerve. (Fig. 26, F.C.N.).

This lies very close to the emergence of the pallial nerve, but is quite distinct from it.

10. Foramen of anterior head retractor nerve. (Fig. 26, F.A.H.).

This lies a little lateral to the foramen magnum. The anterior head retractor nerve gives off one or two fine branches before emerging from the cartilage, but the emergence of these cannot easily be seen.

Two pairs occur on the anterior part of the dorsal surface of the statocyst cartilage; to see these foramina it is necessary to cut the cephalic cartilage into two symmetrical halves, and remove the brain from one of them. They lie just anterior to the transverse ridge which projects

from the statocyst cartilage between the visceral and pedal ganglia. They are:—

11. Foramen of nerve of crista statica.

12. Foramen of nerve of macula statica, which lies just mesial to the foramen of the nerve of the crista statica. Both these foramina lead into the statocyst.

In addition to the foramina of the nerves, there are two pairs of foramina which serve for the passage of blood vessels through the cephalic cartilage. Both pass from the orbit to the ventral side at the edge of the statocyst cartilage, and allow veins to pass from the orbit to enter the cephalic vein. These foramina are:—

13. Foramen of ophthalmic vein. (Fig. 27, F.V.E.).

14. Foramen of vein from head sinuses (F.O.V.) which is a large foramen, a little anterior and mesial to the foramen of the ophthalmic vein.

2. Brachial Cartilage.

Figure 27 shows the brachial cartilage (BR.C.) in the position it occupies relative to the cephalic cartilage. In Figure 29 it has been drawn out of place so that it may not obscure the cephalic cartilage.

It lies a short way anterior to the bridge of the orbital cartilage and ventral to the trochlear cartilages. It has a fairly broad posterior surface, from which three curved prongs project forward. Two of these lie laterally and symmetrically while the third is ventral and median. Each of the lateral prongs bears a slight groove on the antero-dorsal surface along which a fork of the brachial artery runs.

3. Radula Cartilages. (See section on RADULA, page 63.)

4. Horseshoe Cartilage.
5. Sclerotic Cartilage.
6. Equatorial Cartilage.

(See section on **Eye**, page 121, *et seq*).

7. Nuchal Cartilage.

This cartilage is shown isolated in Figure 34, and in transverse section in Figure 24 (N.C.). In Figure 79 (N.C.) it is shown in longitudinal section. It is situated on the dorsal surface of the neck, and its ventral surface is firmly attached to the muscles in this region. It is roughly crescent-shaped, quite thin, and its margin is slightly ridged on the ventral side where the collar muscles (Fig. 34, I.C.F. and O.C.F.) have their origin. A groove (G.N.C.) runs longitudinally down the centre of it.

8. Dorsal Cartilage

This cartilage is shown completely isolated in Figure 35, and in transverse section in Figure 24 (DO.CA.). The main part of it which lines the anterior part of the mantle cavity immediately dorsal to the nuchal cartilage is similar in shape to the latter. A longitudinal ridge (Fig. 35, R.D.C.) which runs down the centre of it fits into the corresponding groove in the nuchal cartilage. These two cartilages fit closely together and prevent water from escaping *via* this part of the neck, when it is being expelled from the mantle.

The dorsal cartilage is continued posteriorly round the margin of the shell as a thin and rather indefinite but tough membrane, strengthened by cartilage, and on which the muscular mantle and the retractor muscles of the head and funnel have their origin.

9 and 10. Funnel and Mantle Cartilages.

These cartilages are shown in surface view in Figure 5 (F.C. and M.C.), and in transverse section in Figure 24. The funnel cartilages are paired and situated sym-

metrically on the posterior part of the ventral wall of the funnel. They are oval in outline, and hollowed out. The actual cartilage is surrounded by a small membranous flange. The mantle cartilages occupy a corresponding position on the inner surface of the mantle wall, and consist of little cartilaginous protuberances. The funnel and mantle cartilages together form a locking mechanism similar to that formed by the dorsal and nuchal cartilages, which prevents water from escaping between the ventral wall of the funnel and the mantle wall, when it is being expelled through the efferent siphon of the funnel. (Fig. 24, E.S.F.)

According to Marmet (1935) these cartilages occur, though in rather varied form, in many Decapods, and in some Octopods. A remarkable feature about them is that the funnel and mantle cartilages develop quite separately, without being in contact, since in the embryo the mantle grows forwards over the visceral dome from the posterior end, and by the time it has extended far enough anteriorly to cover the posterior part of the funnel, both the funnel and mantle cartilages are well developed. Thus there can be no moulding of one part to fit the other during development.

The separate development of two reciprocal parts which function only in the adult, and which, independent of each other, would serve no useful purpose is termed coadaptation, and raises interesting problems in connection with the mechanism of evolution. If it is attempted to explain the evolution of these cartilages by the theory of mutation alone, the imagination is strained by the series of improbabilities which have to be admitted. Since individually neither of these two cartilages would serve any useful purpose, if one or other of them were developed separately it would not be preserved. Yet it is difficult to conceive of their being formed simul-

taneously by mutation, and in such a way that, though quite dissociated in the embryo, at maturity they came to lie exactly opposite each other, and at the same time to have such a form as to fit into each other well enough to procure their preservation through the advantage they bestowed on the individual. Thus one is tempted to fall back on the almost discarded theory of inheritance of acquired characteristics.

11. Diaphragm Cartilage.

Figures 23 and 24 show the position of this cartilage (D.CA.) and it is shown completely exposed in Figure 33. It is a thin oblong structure, tapering at the posterior end, and lying along the mid-ventral line of the anterior part of the visceral dome. It lies immediately dorsal to the cephalic vein. It is perforated anteriorly by a median foramen (Fig. 33, F.A.V.) through which the anterior azygos vein passes to the cephalic vein, and about the middle of its length by paired foramina through which pass the visceral nerves (V.N.).

Anteriorly this cartilage is bound by connective tissue to the ventral surface of the statocyst cartilage. The muscular walls of the cephalic vein are attached to its edges. It is held in place by the retractor muscles of the head (R.H.), which are attached to its edges along its entire length.

12. Fin Cartilages.

The paired fin cartilages (Figs. 30, 31, FI.C.) lie on either side of the trunk. They extend from a little posterior to the anterior margin of the mantle to nearly the extreme posterior end of the animal. Each fin cartilage is long and narrow, and its inner surface is slightly curved concavely so that it fits against the mantle wall. The outside bears a prominent longitudinal ridge to which the

swimming muscle of the fin is attached. This ridge is perforated from the outer surface by the blood-vessels and nerves which supply the fin muscle. Towards the posterior end, the width of this cartilage after gradually increasing, sharply decreases. At this end an impression shows on the inner surface where the retractor muscle of the fin cartilage (Fig. 31, R.F.C.) is attached. The inner surface of the rest of this cartilage is quite smooth, as no muscles are attached to it.

13. BRANCHIAL CARTILAGES.

These are delicate little curved rods (Fig. 54, BR.CA.), which project from the sides of the branchial gland to the extremities of the laminae of the branchia. They form part of the mechanism by which the laminae of the branchia are held expanded so that there may be free access of water to their surface.

MUSCULAR SYSTEM.

The muscular system of *Sepia* is highly developed. The animal can swim with delicate control, and also propel itself backwards through the water with swift darting movements. It has eight powerful, and very flexible and extensible arms for holding its prey, and can project its tentacles with lightning speed, when catching the agile crustacea and small fishes on which it feeds. There are numerous though rather delicate eye muscles, which are capable of moving the eyeball, though the extent of the movement appears to be less than in the case of most fishes.

Systems of muscles can be recognised associated with the following parts of the body:

A. Muscular mantle.

B. Fins.

C. Branchiae.
D. Funnel.
E. Neck.
F. Arms and tentacles.
G. Suckers.
H. Buccal mass.
I. Eyes.

A. Muscular Mantle.

According to Naef (1921) the primitive Cephalopod did not have a muscular mantle such as is present in *Sepia*. This structure appears to have replaced the shell and mantle of the ventral wall of the living chamber of the primitive shell (Text fig. 4a, PR.M., page 12). In *Sepia* the mantle (Figs. 25, 32, M.M.) has its origin round the horny margin of the shell (SH.), on the dorsal cartilage. Posteriorly the two sides of the mantle are united. Anteriorly they are held in place by the crescent-shaped part of the dorsal cartilage (Fig. 24, DO.CA.), which has to withstand the great tensile forces exerted when the mantle is violently contracted. The ventral part of the mantle (Fig. 24, M.M.) consists of a thick sheet of muscle. It is not only used to eject water through the funnel when the animal darts backwards, but is responsible for the continual circulation of water in and out of the mantle for normal respiration.

B. Muscles of Fins.

These consist of the swimming muscle of the fin (Fig. 32, FI.) and of the muscles and membranes (Figs. 31, 32.) which fasten the fin cartilage to the mantle wall, and resist the strain tending to displace it.

[DISSECTION.—*To remove the fin together with the muscles and membranes which hold it in place, first remove the skin on both sides, from the middle of the back and mantle respectively, to the margin of the fin. Then free the lateral*

membranes (Fig. 31, D.F.ME. *and* V.F.ME.) *holding the fin cartilage to the body. Sever the posterior conjunctive fin muscle* (Fig. 32, P.F.M.) *in the mid-dorsal line. Cut away the posterior retractor muscle of the fin cartilage* (Fig. 31, R.F.C.) *from the posterior end of the mantle, in the neighbourhood of the rostrum of the shell, and sever the dorso-lateral fin muscle* (D.F.M.) *at its origin at the point where the nerves to the fin pass through the mantle wall.*]

The swimming muscle consists of two sheets (Fig. 30), one dorsal and one ventral, separated in the middle by connective tissue. Both the dorsal and ventral surfaces of this muscle show parallel ribs running at right angles to the fin cartilage. The muscle is attached throughout its length to the longitudinal ridge of the fin cartilage. Muscle fibres run in three directions, longitudinally, at right angles to the fin cartilage, and perpendicular to the plane of the fin.

The fin cartilage is held in place by two tough membranes, the dorso-lateral and the ventro-lateral fin membranes (Figs. 31, 32, D.F.ME.; Fig. 31, V.F.ME.) which are attached one dorsally and the other ventrally, to the cartilage at the base of the fin muscle, and stretch over the surface of the back and ventral part of the mantle respectively. The ventro-lateral membrane is slightly muscular throughout its length. The dorso-lateral membrane is reinforced by a well developed dorso-lateral fin muscle (Figs. 31, 32, D.F.M.) which has its origin on the mantle wall at the point where the nerves from the pallial nerve emerge through the wall of the mantle. This muscle is inserted on to the fin cartilage at the base of the swimming muscle. It follows the course of the nerves (Fig. 31, F.N.) to the swimming muscle, and its function is probably chiefly to protect these nerves.

Posteriorly the two fins are joined together by a very strong conjunctive muscle (Fig. 32, P.F.M.), made up of

parallel transverse bands. This muscle is attached to the dorsal edge of the posterior part of the fin cartilage. On to the inner surface of the tapering posterior part of the fin cartilage is inserted the strong retractor muscle of the fin cartilage (Fig. 31, R.F.C.) whose origin is fused with the posterior part of the mantle. Thus the fin cartilage is held very firmly at the posterior end, where it lies against the posterior part of the shell margin. Anteriorly where it lies against the mantle wall, the attachment is quite loose.

C. **Structure of the Branchiae.** (Figs. 25, 54, 81.).

The main axis of each branchia consists of a laterally compressed retractor muscle (Fig. 25) which has its origin on the posterior part of the mantle wall close to the margin of the shell. This muscle first runs forwards attached to the side of the visceral dome. At the base of the branchia it divides into two, an axial part (Figs. 25, 54, A.R.B.) which is the larger, continuing straight forward, while the much narrower ventral part (Figs. 25, 54, M.R.B.) travels round the edge of the visceral dome to the ventral side, and forms the ventral edge of the axis from which the laminae branch out.

This ventral muscle, which is closely associated with the efferent branchial blood-vessels (Fig. 54, E.V.), has a pinnate form, sending branches along the ventral edge of each of the laminae of the branchia. At its distal end each of these branches is attached to the end of the little branchial cartilage (BR.CA.) which projects from the side of the branchial gland. The respiratory filament (Figs. 53, 54, R.F.B.) is attached mesially to the axial muscle by a delicate membrane (Fig. 54, M.R.F.), the whole forming a structure which enables the respiratory surface of each of the laminae of the branchia to be so held that it has free contact with the water which enters the mantle cavity. The branchial gland (Figs. 25, 54, 81, B.GL.) which runs in the main

axis of the branchia dorsal to the axial muscle, is loosely attached to the mantle wall for most of its length by an elastic membrane (Fig. 54, BR.M.), reinforced at its anterior end by a stout muscular cord, the branchial ligament, so that the whole branchia lies loosely within the mantle cavity. From the structure of the branchiae it appears that *Sepia* would be able to restrict considerably respiration in contaminated water, by folding up the branchiae instead of expanding them.

D. Muscles of Funnel.

The musculature of the funnel of certain dibranchiate Cephalopods formed part of a phylogenetical study by Brock (1880), and included in this work is a good description, with figures, of the funnel musculature of *Sepia officinalis.*

[DISSECTION.—*Refer to the description of* Fig. 23, page 173.]

The funnel of *Sepia* consists of three parts, a median exhalent siphon (Fig. 24, E.S.F.), and a pair of lateral valves (L.P.), consisting of muscular walled chambers, which are stretched by the pressure of water being forced out of the mantle cavity during exhalation, so that they completely block the sides of the opening through which the water enters. The following muscles can be recognised:

1. Retractor muscles.
2. Outer collar muscles.
3. Inner collar muscles.
4. Anterior adductor muscles.
5. Posterior adductor muscles.
6. Lateral adductor muscles.
7. Transverse muscles.

Figures 23 and 25 show dissections of the funnel, while in Figure 24 it is shown in transverse section.

1. RETRACTOR MUSCLES. (Figs. 23, 25, R.FU.).

These are the largest and most powerful muscles of the funnel. They have their origin at about the middle of the shell margin. At their origin they are fused with the retractor muscles of the head (Fig. 25, R.H.), and the walls of the mantle (M.M.). They run forward on either side of the visceral dome, and in the region of the funnel cartilages (Fig. 23, F.C.) merge into the dorsal and ventral walls of the exhalent siphon.

2. OUTER COLLAR MUSCLES. (Figs. 23, 24, 25, O.C.F.).

These muscles have their origin on the edges of the nuchal cartilage, and fuse with the ventral wall of the exhalent siphon. They form the outer walls of the lateral valves.

3. INNER COLLAR MUSCLES. (Figs. 23, 24, 25, I.C.F.).

These muscles are formed partly by the forking of the retractor muscles of the head (see Fig. 23, I.C.F.), while the origin of the anterior part is at the edge of the nuchal cartilage, mesial to the outer collar muscles. They fuse laterally with the dorsal wall of the exhalent siphon, and form the inner walls of the lateral valves. Anteriorly the inner and outer collar muscles are continuous (Fig. 34, I.C.F. and O.C.F.).

4. ANTERIOR ADDUCTOR MUSCLES. (Fig. 23, A.A.F.)

These are a pair of broad flat muscles which have their origin on the posterior face of the brachial cartilage, close to the middle line. They run, with fan-like expansion, postero-laterally to their insertion on the dorsal wall of the exhalent siphon.

5. POSTERIOR ADDUCTOR MUSCLES. (Fig. 23, P.A.F.)

In *Sepia* these muscles arise as a single muscle from the posterior surface of the bridge of the cephalic cartilage. It is a slender muscle which passes ventrally and to the right

of the cephalic vein. It then broadens and forks into two muscles which run forwards, and are inserted on the dorsal wall of the exhalent siphon.

6. LATERAL ADDUCTOR MUSCLES. (Fig. 23, L.A.F.)

These consist of broad but weakly developed sheets of muscle lying just under the skin on the ventral side of the head, which stretch from their origin at the bases of the ventral arms to their insertion on the ventral wall of the exhalent siphon.

7. TRANSVERSE MUSCLES. (Fig. 23, T.M.F.)

These are dorso-laterally flattened well defined bands of muscle which have their origin on the edge of the diaphragm cartilage, and run transversely to the posterior part of the dorsal wall of the exhalent siphon where they are inserted.

E. Muscles of neck.

[DISSECTION :—*See description of* Fig. 25, page 173.]

Comparative anatomy shows that in the more primitive state of cephalopod organisation there were two pairs of neck muscles, the lateral and the median dorsal retractor muscles of the head. But in *Sepia* it is only possible to distinguish a single very large pair, probably owing to fusion.

The retractor muscles of the head are shown in Figures 23, 24 and 25 (R.H.). They have their origin at the edge of the shell at about the middle of its length. At their origin they are fused with the retractor muscles of the funnel and with the mantle wall. Posteriorly these muscles lie lateral to the visceral dome, and as they run forward they gradually expand over the ventral surface of the liver. At about the posterior limit of the funnel they attach to the edges of the diaphragm cartilage

(Fig. 23, D.CA.), and form a capsule completely enclosing the anterior part of the liver on the ventral side. In this region the inner collar muscles (I.C.F.) are given off as lateral branches.

They are firmly attached to the ventral side of the nuchal cartilage close to its margins and just mesial to the attachment of the inner collar muscles. Towards the anterior end of the former, the bulk of the retractor muscles is increased by fibres whose origin is on the whole ventral surface of the nuchal cartilage, so that they become completely fused on the dorsal side into a continuous muscular sheath. On this side the fibres of these muscles are partly attached to the cerebral cartilage and partly continuous with the bases of the arms. On the ventral side they are inserted partly on to the posterior surface of the orbital cartilages and bridge of the skull (Fig. 27, O.C. and B.R.; Fig. 25, unlettered), and partly on to the posterior surface of the brachial cartilage (Fig. 25, BR.C.), where the right and left muscles are fused together.

F. Muscles of Arms and Tentacles.

[DISSECTION.—*The muscle zones of the intrinsic muscles of the arms and tentacles can be roughly made out from hand sections, but to see them clearly it is necessary to examine microtome sections. These can be made from quite young specimens of about 12 mm. length. In sections made from such specimens the brachial nerves appear very large in proportion to the rest of the arms.*]

1. ARMS.

The anterior part of the head consists of a hollow cone of muscle (Fig. 36) formed by the closely united bases of the arms. This cone has its origin dorsally on the cerebral cartilage (Fig. 29, CE.C.), laterally on the lateral ligaments (Fig. 28, L.F.O.) and ventrally on the anterior and lateral

surfaces of the brachial cartilage (Fig. 27, BR.). On the dorsal side continuations of the retractor muscles of the head also contribute to its formation. The apex of the cone is just anterior to the anterior end of the brain. From this point it expands forwards enclosing the peri-buccal sinus (Fig. 36, P.B.S.) in which lies the buccal mass (B.M.).

The cone divides into eight arms (Fig. 3, A 1–4) which surround the mouth. The bases of the intrinsic muscles of all the arms are bound together by a continuous sheath of muscle, the extrabrachial muscle (Fig. 80, unlettered), which continues to the top of each arm as a thin sheath (Fig. 50, E.A.M.) round the intrinsic muscles. The extrabrachial muscle tissue also contributes to the inter-brachial webbing (Fig. 7, I.W.) which joins the proximal parts of the arms together. The muscular buccal funnel (Fig. 7, B.F.) is fastened to the base of each of the arms by radially placed buccal pillars. The buccal pillars of the two dorsal arms have become fused.

The arrangement of the intrinsic muscles of the arms is shown in Figure 50. Around the central brachial nerve (B.N.) there is a wide zone (R.M.A.) of interlaced fibres which run more or less radially. Through the periphery of this zone run large clearly marked bundles of longitudinal fibres (L.M.A.). Outside this region there are two layers of laterally placed oblique muscles (O.M.A.), which do not, however, extend right round the arm. The whole of these muscles is encased by a sheath of longitudinal extrabrachial muscle fibres (E.A.M.).

2. TENTACLES.

The tentacles have their origin on the posterior surface of the brachial cartilage (Fig. 25, TEN.). They arise close together near the middle line. Normally they lie neatly packed within the tentacle pockets (T.PO.), but they are, like the arms, highly muscular, and can be shot out swiftly and accurately to catch prey (Fig. 2).

Their musculature (Fig. 51) is very similar to that of the arms. The chief difference is that in place of the two lateral layers of oblique muscle found in the arms, there is a rather indefinite zone of circular fibres mixed with those which radiate from the central zone (R.M.T.) round the nerve (T.N.). This zone extends right round the region of the bundles of longitudinal fibres (L.M.T.). The intrinsic muscles of the tentacles are also encased in a sheath of extrabrachial muscle. (E.T.M.)

G. Muscles of Suckers.

The arrangement of the muscle fibres in the suckers, and their functions are described in great detail by Guérin (1908). As it is necessary to employ histological technique to study the minute structure of the suckers, it is only possible to give a broad outline here.

Figures 13 and 14 show views of a typical sucker. It consists of a mechanism working rather like a cylinder and piston. The cylinder or sucking chamber (SU.C.) is supported by a chitinous horn ring (H.R.), the mouth of which bears a chitinous and finely toothed attachment flange (A.SU.) on the outside. The piston or sucking pad (SU.P.) consists of a muscular pad, concavely hollowed on its surface, which projects from the floor of the sucking chamber. An annular muscle (C.SU.) encircles the base of the horn ring. Each sucker is attached to the arm by a short muscular stalk up the centre of which runs the sucker nerve. By the action of the sucker muscles, the volume of the sucking chamber can be diminished and then expanded, and thus a partial vacuum obtained. The suckers vary considerably in the details of their form, according to the part of the arms or tentacles from which they are taken. This polymorphism is dealt with in detail by Naef (1921).

H. Muscles of Buccal Mass.

In the buccal mass three groups of muscles can be recognised:

(*a*) Retractor muscles of buccal mass.

(*b*) Jaw muscles.

(*c*) Radula muscles.

(*a*) RETRACTOR MUSCLES OF BUCCAL MASS.

The buccal mass is held loosely in place, partly by the tough and somewhat muscular membrane (Fig. 36, M.O.L.) which forms the outer lip, and is reflected back and firmly attached to the walls of the peri-buccal sinus (P.B.S.), and partly by two pairs of retractor muscles (L.M.B. and O.M.B.).

[DISSECTION.—*Open the peri-buccal sinus by a longitudinal mid-ventral incision, and free the buccal mass anteriorly. Cut away the bases of the arms on one side.*]

1. Oblique retractor muscles. (Fig. 36, O.M.B.).

These are the outermost, and have their origin near the middle line on the dorsal wall of the peri-buccal sinus. They are broad and delicate bands of muscle, which curve round the buccal mass to their insertion on its anterior ventral surface close to the middle line. For much of their length they lie quite freely except for the attachment of their postero-ventral margins to the underlying lateral retractor muscles.

2. Lateral retractor muscles. (Fig. 36, L.M.B.).

These lie immediately within the oblique muscles. Their origin is at the posterior dorsal wall of the peri-buccal sinus. From here they travel forwards as a thin but very broad sheet of muscle, which forms an almost complete cone surrounding the anterior part of the buccal mass,

to their insertion on the surface of the anterior part of the latter. These muscles and the membrane to the outside of which they are attached delimit the peri-oesophageal sinus (P.O.S.), the anterior part of which they enclose, from the peri-buccal sinus (P.B.S.) which lies outside and round them. These muscles do not extend posteriorly over the ventral surface, and so here only the membrane separates the two concentric sinuses.

The buccal mass can be moved forwards to some degree by the contraction of the muscular case, formed by the bases of the arms, in which it lies. Rotation is achieved by the action of the oblique muscles, and retraction by the lateral retractors.

(*b*) JAW MUSCLES.

The jaw muscles (Fig. 37, M.J.) form a solid sheath in which the horny jaws are encased. Individual muscles cannot be recognised. The fibres which open the jaws lie longitudinally on the dorsal and ventral surfaces of the buccal mass, while the rest of the muscular tissue serves to exert the considerable forces which are required in crunching up crustacea.

(*c*) MUSCLES OF RADULA (see section on RADULA, page 63).

I. **Muscles of Eye.**

There are two systems of muscles associated with the eye. These are:

1. Extrinsic muscles of the eyeball, which consist of 13 oculomotor muscles.
2. Intrinsic muscles of the eyeball, which consist of the ciliary muscle, and the sclerotic and retinal muscles.

For the description of these muscles, see section on **Eye**, page 121 *et seq.*

RADULA.

[DISSECTION.—*The structure of the radula is most easily seen by isolating it, together with the palatine lobes and tongue* (*see* Fig. 41) *from the rest of the buccal mass, and then making a series of hand sections through it.*]

The radula (Figs. 39, 40, 41) consists of a horny toothed cuticle (Fig. 40, H.R.M.) attached to the radula membrane (R.M.) which fits over an odontophore (Figs. 40, 41, OD.). The latter is a muscular structure, U-shaped in cross section, which projects forwards from the posterior part of the jaw muscles. It is reinforced by paired cartilaginous rods (Figs. 40, 41, R.C.), and its function is to support the radula. Anteriorly the radula membrane fits loosely over it, and is not attached to it. Posteriorly the radula membrane is bound to the neighbouring tissues. There are two sets of muscles, both lying in the radula membrane which serve to work the radula. The ventral pair (A.R.), which are the adductor muscles, tend to pull the radula out of the radula sac, while a pair of dorsal retractor muscles (R.R.) pull it in the opposite direction. Thus the radula can be pulled to and fro over the odontophore. The radula sac, in which the radula teeth, and the horny cuticle to which they are attached, are secreted, lies in the longitudinal depression between the two arms of the U-shaped odontophore. Posteriorly this sac, which contains the radula gland (Fig. 41, R.G.), is cylindrical in shape, and the teeth are secreted within it.

The radula itself bears seven longitudinal rows of teeth (Fig. 42.). The secretion of these teeth is continuous, and the whole radula gradually shifts forwards. On the oldest part of the radula the teeth are quite blunt through wear, and this part falls away from the radula membrane as the radula grows forward.

The radula does not appear to be used for rasping, as the large fragments of crustacean shells which are usually

found within the stomach, do not show any signs of being rasped. Yet the fact that the older teeth are worn and blunt indicates that it is used for some purpose. It is probably employed to assist in swallowing, by pushing the food into the groove (Fig. 37, G.O.) between the palatine lobes (P.L.) which leads to the oesophagus (OES.).

DIGESTIVE SYSTEM.

The digestive system is well developed and highly differentiated. There are very powerful horny jaws for breaking up the food, a long oesophagus, a muscular stomach, a blind caecum, and a short, slightly looped intestine. The digestive juices are derived from three sources; the very large digestive glands; the so-called pancreatic appendages of the ducts of the digestive glands, which open into the caecum; and from the walls of the caecum. Although the caecum plays some part in absorption, this is stated to take place chiefly in the digestive glands. A remarkable feature of the digestive system is the so-called salivary glands. These play no part in digestion, but are in reality poison glands, and their secretion acts on the central nervous system of *Sepia's* prey, causing almost instantaneous paralysis.

A. Alimentary Canal.

[DISSECTION.—*See description of Figs.* 36, 37, 46.]

In the alimentary canal the following regions can be recognised:

1. Mouth and buccal cavity.
2. Oesophagus.
3. Stomach.
4. Vestibule.
5. Spiral caecum.
6. Intestine.
7. Rectum and anus.

1. Mouth and Buccal Cavity.

Figure 37 shows a view of the mouth cavity which has been exposed by the removal of the dorsal half of the buccal mass. The buccal mass is shown in median longitudinal section in Figure 49, and more simplified in Figure 79. Figure 80 shows it in transverse section. The mouth is surrounded by a fleshy and papillated circular lip (Figs. 37, 49, 79, I.L.). Within this lip lie a pair of very powerful horny jaws, the form of which can be ascertained by comparison of Figures 37, 38 and 44. The ventral jaw overlaps the dorsal. The posterior and peripheral parts of these jaws are embedded within the muscles of the buccal mass, but the roof of the mouth is formed entirely by the inner concave surface of the dorsal jaw (Fig. 80. D.J.)

At the centre of the tip of the so-called tongue, which projects anteriorly into the ventral part of the buccal cavity, the duct of the posterior salivary glands (Fig. 37, O.P.S.) opens. The surface of the tongue is papillated and glandular. The radula (described on page 63) lies immediately dorsal to the tongue.

The palatine lobes (Figs. 37, 41, P.L.) arise just dorsal to the tongue. They are paired fleshy structures which project dorsally on either side of the radula. Except at their anterior ends, they are bound to the central mass of the mouth, and the groove (Fig. 37, G.O.) which lies between them leads to the oesophagus. The inner surface of these lobes is lined with chitin, which on the anterior part bears small backward-projecting spines (Fig. 49, unlettered). This chitin is attached to the inner surface of the dorsal jaw, which forms the dorsal surface of the buccal cavity, and is continuous with the chitin (Figs. 37, 38, H.OES.) which lines the entire oesophagus and stomach. The anterior salivary glands open by orifices (Fig. 37, O.A.S.) on the inner surface of the palatine lobes on either side of the radula.

2. OESOPHAGUS. (Figs. 36, 49, 79, OES.)

This is a long and slender tube with quite thin walls, and lined throughout its length with chitin. It runs from the posterior end of the buccal mass straight back to the stomach. The anterior part of it lies quite freely in the peri-oesophageal sinus (Figs. 36, 49, P.O.S. Fig. 79, S.) which extends to the posterior limit of the skull (Fig. 36, C.C.) and passes through the centre of the brain (see Figs. 49, 56, 57, OES.). After passing through the membrane which closes the foramen magnum at the posterior end of the skull, the oesophagus runs along the middle line between the two digestive glands (Figs. 36, 49, 79, L.), and near the dorsal side of the visceral dome.

3. STOMACH. (Figs. 20, 21, 36, 46, ST.)

The stomach is a muscular bag into which the oesophagus opens by a sphincter valve (Fig. 46, S.O.). The entire stomach is lined with chitin (H.S.). This lining is comparatively thin except in the region of a very powerful grinding muscle (C.M.S.) which encircles the stomach transversely. On the left side the stomach communicates with the vestibule, the opening into the latter being controlled by a sphincter muscle (S.S.). A very large gastric ganglion (Fig. 36, G.G.) is attached to the ventral wall of the stomach, near the angle formed by the oesophagus and the intestine.

4. VESTIBULE. (Fig. 46, V.)

This is the chamber with which the stomach (ST.), the caecum (CA.) and the intestine (IN.) all communicate. Three sphincter valves, of the stomach (S.S.), of the caecum (S.C.) and of the intestine (S.I.) respectively, control between them the direction in which the contents of the stomach and caecum shall move. If the sphincters of the stomach and intestine are relaxed, the hard shelly residues can be expelled from the stomach without entering the

caecum (large particles of solid matter are never found in the caecum). Semi-digested food can flow from the stomach to the caecum when the stomach and caecum sphincters are relaxed, while relaxation of the caecum and intestine sphincters allows the contents of the caecum to travel into the intestine.

5. SPIRAL CAECUM. (Figs. 20, 21, 46, CA.)

This is slightly coiled about a columella. Its surface is greatly increased by the pleating (L.CA.) of its lining. These pleats vary in size, some stretching from the columella to the periphery, while others are interspersed between them, and fill the gaps between the larger ones in the peripheral region. These pleats, which are glandular, are ribbed on both sides (Fig. 45). This is evidently further to increase the surface area of the lining of the caecum. The single duct (Fig. 46, D.L.), formed by the junction of the ducts of the paired digestive glands close to the caecum, opens into the latter in the columella region (Fig. 46, O.D.L.). The opening is guarded by two valves. The dorsal valve is formed by the beginning of one of two ridges (R.IN.) which run up the dorsal wall of the intestine. The ventral valve is formed by a little flap of tissue (G.C.S.) which runs from the columella over the ventral surface of the caecum to the posterior part of the sphincter of the stomach, and forms a groove along which it appears that the secretion from the duct of the digestive glands can flow directly to the stomach.

6. INTESTINE. (Figs. 21, 36, 46, IN.)

The intestine is very short. It travels anteriorly for a short way from the vestibule, and then exhibits a kink (Fig. 36, IN.) before merging into the rectum (Fig. 5, RE.) which is loosely attached to the ventral wall of the visceral dome (Fig. 23, A.RE.). It is lined with glandular epithelium, and two very prominent ridges run up the inside of its

dorsal surface. One of these arises in the region of the columella of the caecum, and the other in the vestibule. These ridges lie close together and thus a groove is formed between them.

7. RECTUM AND ANUS. (Figs. 20, 43, RE.; Fig. 5, RE. and AN.)

There is no distinct differentiation between the intestine and rectum. In the anterior part of the rectum the two ridges, which are so prominent in the intestine, disappear. In the anal region the rectum is closed by a sphincter valve (Fig. 43, S.RE.). Just anterior to this the duct (D.I.) of the inksac opens into it. At the sides of the anus a pair of leaf-like structures (AN.V.), the anal valves, project. It is difficult to assign any function to these in the adult, but in the case of *Loligo pealii*, Williams (1909) has observed in young transparent specimens of 5 to 6 mm. length, that there was rhythmical waving of these structures, synchronised with opening and closing of the rectal sphincter, whereby a current of water passed into the rectum. It was found that carmine particles, placed in the water in which the animal was swimming, were introduced into the rectum, and transported back by ciliary action to the anterior part of the intestine. Williams suggests that food particles introduced in this way might be absorbed intracellularly. It therefore appears that the anal valves may form part of a feeding mechanism in young specimens.

The walls of the caecum, the intestine, and the rectum are lined with cilia.

B. Glands Opening Into Alimentary Canal.

The following glands open into the alimentary canal:

1. Sublingual gland,
2. Anterior salivary glands,

3. Posterior salivary glands,
which open into the buccal cavity.

4. Hepato-pancreas,
which opens into the spiral caecum.

5. Ink gland,
which opens into the anterior end of the rectum.

1. SUBLINGUAL GLAND. (Fig. 41, G.T.)

This consists of glandular tissue lying on the ventral side of the tongue. This tissue has no special duct, and secretes directly into the buccal cavity. Its function is unknown.

2. and 3. ANTERIOR AND POSTERIOR SALIVARY GLANDS.

The anterior salivary glands (Figs. 41, 49, 79, A.S.G.) are comparatively large paired glands contained within the palatine lobes of the buccal mass. They extend throughout the whole length of the palatine lobes. Anteriorly they occupy the whole of each lobe, but posteriorly they are limited to the dorsal part. A duct (Fig. 41, D.A.S.), which can be seen in transverse hand sections, runs through the centre of each gland. The glands open on either side of the radula (Fig. 37, O.A.S.). In fresh specimens the location of the apertures of these glands is facilitated by placing the opened buccal mass in water and then squeezing the palatine lobes, when a cloudy stream of the secretion is forced out, but in preserved specimens the secretion of these glands becomes coagulated, and will not flow out when they are squeezed.

The posterior salivary glands (Figs. 25, 36, 49, 79, P.S.G.) lie close against the oesophagus, just posterior to where it passes through the membrane which closes the foramen magnum of the skull; they are sandwiched between the anterior part of the digestive glands and the oesophagus. Their ducts (Figs. 36, 49, D.S.G.) pass through the membrane surrounding the foramen magnum, and enter

the peri-oesophageal blood sinus (P.O.S.). The paired ducts then unite to form a single duct which floats freely in the sinus and runs forwards ventral to the oesophagus, to enter the postero-ventral surface of the buccal mass in the mid-ventral line. After passing through the muscles of the buccal mass it opens into the buccal cavity at the tip of the tongue (Fig. 37, O.P.S.).

Both of the salivary glands have been misnamed. Neither of them, according to Romijn (1935) and many earlier investigators, secretes any digestive enzymes. Both are really poison glands. Krause (1895) was the first to establish the poisonous nature of the posterior salivary glands, and de Rouville (1910) says that the secretion of the anterior salivary glands of Cephalopods in general is also poisonous. According to Livon and Briot (1906) this poison acts on the central nervous system of the prey. These authors record that in the case of *Octopus*, the prey has been observed to be paralysed merely by the approach of the former.

4. HEPATO-PANCREAS. (Figs. 24, 81, L.: Fig. 36, L., D.L. and PA.: Figs. 49, 79, L. and D.L.)

This term is used to describe the digestive glands and the appendages which are attached to their ducts.

The paired digestive glands, often referred to as the liver, are very large. They lie close together, extending back from immediately posterior to the cephalic cartilage, and fill the anterior half of the visceral dome. Anteriorly they are transversely cleft, where the pallial nerves (Fig. 36, P.N.) pass through them. Their pointed posterior ends lie on either side of the anterior part of the body cavities.

The ducts (Figs. 36, 49, 79, D.L.) of the digestive glands are given off from the mesial surface towards the ventral side, and about three-quarters of the total length of the

glands from their anterior ends. These ducts immediately enter the dorsal chamber of the renal sac (Fig. 21, D.L.), and travel to the caecum (Figs. 21, 36, CA.), passing one on either side of the intestine (IN.). (The exact course of these ducts within the renal sac and their attachment are described in the section on the dorsal renal chamber, page 35.) In the region of the caecum the two ducts unite. Throughout their course in the dorsal renal chamber they bear branching so-called pancreatic appendages (Fig. 36, PA.), which open by quite wide orifices into the main ducts. These ducts are ciliated throughout their length.

There has been much controversy concerning the function of the digestive glands and pancreatic appendages. According to Cuénot (1907) who bases his own conclusions on the evidence of previous work, and on some convincing physiological experiments of his own, the digestive glands perform several functions.

a. They secrete digestive enzymes, which are poured into the caecum and stomach.

b. They excrete waste matter extracted from the blood, by means of mucous threads which travel to the caecum. This process alternates with the secretion of digestive enzymes.

c. They absorb food, liquified by the digestive processes in the stomach and caecum, which is conveyed by peristaltic action along the ducts of the glands.

d. They are also to some extent storage organs.

According to Cuénot the caecum only absorbs fats. Romijn (1935) says that while the secretion of the digestive glands will digest both starch and proteins, the action of the pure secretion of the pancreas is limited to the breaking up of certain amino acids; but when it is activated by the extract of the caecum wall it can break up many proteins.

5. Ink Gland. (Fig. 5, is., Fig. 20, d.is., Fig. 43.)

[Dissection.—*Detach the inksac and the anterior part of the rectum from the visceral dome, and cut them in half in the longitudinal dorso-ventral plane. Wash overnight in a gentle stream of water.*]

The inksac and ink gland of Cephalopods have been studied in great detail by Girod (1882). The ink gland is contained in a large vesicle or reservoir (Fig. 43, r.i.), which lies over the posterior ventral surface of the visceral dome, covered only by the skin of the latter. It leads into a wide duct (d.i.) which runs anteriorly along the right side of the rectum (Figs. 5, 43, re.), which it enters on the dorsal side close to the anus. Just before it enters the rectum the duct bears two circular sphincter muscles (Fig. 43, a.s.i. and p.s.i.) enclosing a small glandular ampulla (a.m.) between them.

The ink gland (c.i.g. and p.i.g.) is attached to the dorsal wall of the posterior part of the vesicle. The central zone (c.i.g.) of the gland is colourless. From this region membranous trabeculae, covered by a secretory epithelium are continuously growing out, which, as they pass towards the ventral and anterior part of the gland, secrete the ink (p.i.g.). The ink is released by the breakdown of the cells which produce it. It escapes through an orifice (o.i.g.) situated towards the anterior end of the ventral wall of the ink gland, and is stored within the reservoir (r.i.) of the inksac. The secretion consists of a colourless plasma, containing a suspension of minute dark brown particles.

According to Girod the process of discharging the ink is as follows. The reservoir is kept full by continuous secretion of the ink gland. Peristaltic action in the duct of the reservoir drives some of the ink up into the ampulla, the posterior sphincter of which opens to allow it to enter. Then this closes and the anterior sphincter opens. By the

contraction of the ampulla a portion of ink is thus introduced into the mantle cavity via the anus. By the regular repetition of this process a steady flow of ink into the mantle cavity can be maintained.

The large artery and vein of the ink gland are shown attached to the inksac in Figure 20 (IS.A.V.).

The ink gland is innervated by a branch of the gastric ganglion, while the contraction of the inksac is controlled by a branch of the visceral nerve.

The common pigment sepia is made from the secretion of the ink gland. It is prepared by dissolving the dried secretion in dilute ammonia or soda, and reprecipitating with hydrochloric acid.

C. Process of Digestion.

The food, consisting chiefly of crustacea, is captured by the tentacles and arms and broken into comparatively large fragments by the jaws. At the same time the prey is paralysed by the secretion of the salivary glands. Swallowing is probably achieved by the action of the radula. In the stomach digestion commences, through the action of enzymes introduced from the hepato-pancreas and caecum. (No digestive enzymes are secreted by the stomach, which is lined throughout with chitin.) In the stomach the digestible part of the food is separated from the indigestible part, consisting chiefly of the shells of crustacea, which are removed directly to the intestine. The semi-digested and more or less fluid food passes into the caecum, where digestion is completed. Absorption is by the walls of the caecum and in the digestive gland, up the ducts of which the liquid and digested food is transported. Some absorption may also take place in the intestine, but the very short length and small surface area of the latter indicate that absorption is not its main function, which

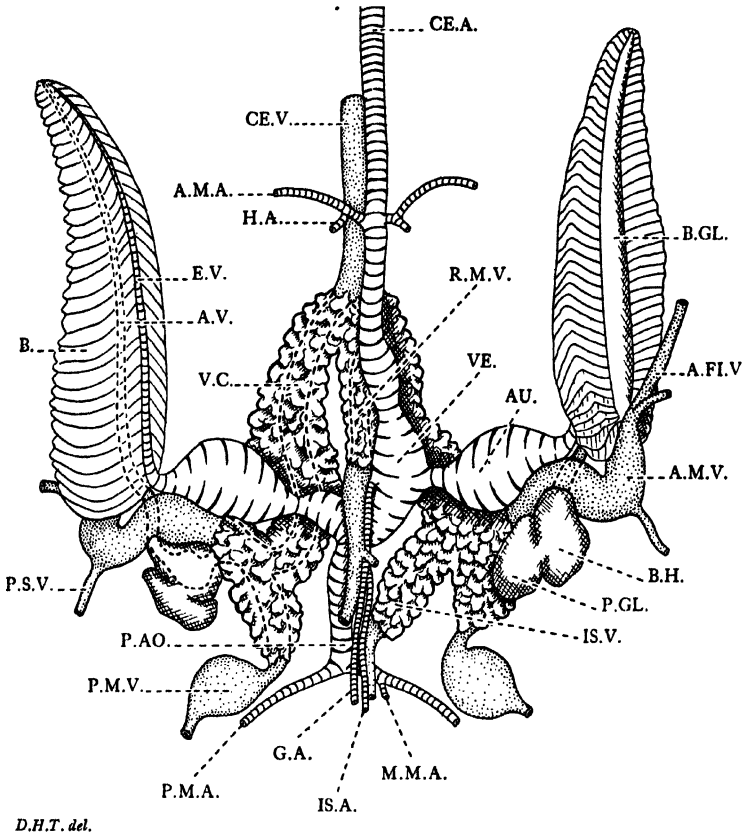
appears to be provision of an easy route for the expulsion from the stomach of the large hard fragments of crustacean shell which accumulate there.

CIRCULATORY SYSTEM.

As in all dibranchiate Cephalopods there are three hearts in *Sepia*. They consist of a pair of single-chambered branchial hearts which propel the blood into the branchiae, and a systematic heart, with paired auricles and a single ventricle, which receives the oxygenated blood from the branchiae and pumps it all over the body.

There are well developed systems of arteries and veins, connected by a network of capillaries. Oxygenated blood from the efferent branchial vessels (Fig. 54, E.V.) of the paired branchiae enters the muscular ventricle (Fig. 47, VE.) *via* thin-walled but contractile auricles (Figs. 47, 54. AU.). Two main arteries, the dorsally situated cephalic artery (Fig. 47, CE.A.), and the posterior aorta (P.AO.) conduct the blood to all parts of the body. In addition to these large arterial trunks two smaller arteries also leave the ventricle. These are a very small anterior renal artery (A.R.A.), and the rather larger genital artery (G.A.).

Unlike the arteries, which have muscular walls and a small bore, the veins have exceedingly thin walls and a large bore. Some of the larger veins are contractile, and there is a great deal of anastomosing among the smaller veins. The large ventrally situated cephalic vein (Fig. 48, CE.V.) returns blood from the arms, and receives the blood which collects in large sinuses (P.B.S., P.O.S. and O.S.) situated in the head region. This vein also receives various other factors. In the region of the renal papillae it forks into two venae cavae (Fig. 48, V.C.), which lead to the branchial hearts (B.H.). The venae cavae receive very large anterior and posterior mantle veins (A.M.V. and



TEXT-FIG. 5. Based on the original by John Hunter.

Key to the Frontispiece.

The figure, which is reproduced here approximately the size of the original specimen, represents in dorsal view an injected preparation showing the following features: the main veins, covered by renal appendages, which lead to the branchial hearts, the branchial hearts themselves with the pericardial glands still attached, the afferent branchial vessels (partly obscured by the anterior mantle veins) leading to the branchiae, the efferent branchial vessels, the two auricles, and the ventricle, with the cephalic artery, the posterior aorta and the genital artery leaving it. The vessels which are given off from the cephalic artery shortly after it leaves the ventricle, the left mesenteric vein and the posterior azygos vein are omitted. The injection has somewhat distended the auricles. The left branchia has been turned round to show the efferent branchial vessel which runs along its ventral side. Although the original drawing was faithfully reproduced in 1834 in the illustrated catalogue of the Museum of the Royal College of Surgeons, accompanied by an accurate and clear explanation, in most subsequent reproductions the afferent branchial vessels have been overlooked, and in all cases the anterior mantle veins have been mistaken for them in the interpretation.

P.M.V.). They also receive various other factors, chief of which are the mesenteric veins (R.M.V. and L.M.V.), while the right vena cava also receives a large vein from the ink gland (IS.V.). The cephalic vein is highly contractile and in the region immediately dorsal to the funnel it expands into a stout-walled chamber (M.CE.V.). All the factors entering this chamber are guarded by efficient valves to prevent back flow, and powerful peristaltic action drives the blood which enters this chamber towards the venae cavae. From the latter hang hollow glandular renal appendages (RE.A.), the lumina of which are continuous with the lumina of the venae cavae. From the venae cavae the blood passes into the branchial hearts (B.H.), which by rhythmical contraction drive the blood through the afferent vessels (Figs. 48, 54, A.V.) into the capillaries of the laminae of the branchiae, where gaseous exchange takes place.

Both in the arteries and the veins small variations occur in respect of the connection between the smaller vessels with the major trunks, but the general scheme of all the major vessels is very constant. An example of these variations is supplied by the median mantle artery (Fig. 47, M.M.A.), which is sometimes given off from the right, and sometimes from the left posterior mantle artery. It may even be given off from the posterior aorta. These variations should be borne in mind when the more detailed description of the arteries and veins is compared with the actual arrangement in any given specimen.

The separation of venous and arterial blood is complete, and all the blood from the veins has to pass through the branchiae before it can enter the arteries. The blood, which contains haemocyanin, is pale blue in the oxygenated state, and colourless in the venous. It contains amoebocytes.

A. Arterial System.

[DISSECTION.—*For satisfactory investigation both of the arteries and veins, it is necessary first to inject the vessels (see page 149 for practical details). The arteries of the posterior part of the visceral dome can be followed by opening up the body cavities. The arteries branching from the cephalic artery immediately after it leaves the heart are most easily seen from the dorsal side, after removing the shell. The best way to follow the arteries supplying the anterior part of the body is by a lateral dissection (see* Fig. 49). *Remove the left liver lobe, and the left half of the head muscles posterior to the arms, leaving the arteries which supply these muscles as far as possible intact. Cut away the left side of the cephalic cartilage so that the brain is exposed, and remove sufficient of the latter to expose the course of the arteries which pass through it. Open the peri-buccal sinus on the* **mid-dorsal** *side by a longitudinal cut between the dorsal arms. The forks of the anterior cephalic arteries* (Fig. 49, A.C.A.) *which run round the ventral wall of the peribuccal sinus can be seen without further dissection if the injection has reached them. The arteries, which go from these vessels up the centre of each arm, can be followed by slitting the arms longitudinally.*]

HEART. (Figs. 21, 52.).

The position of the heart is described in the section on the viscero-pericardial coelom (page 33). It consists of a pair of thin-walled muscular bag-like auricles (Figs. 21, 52, AU.) which open laterally into the ventricle (VE.). Each of these openings is guarded by a pair of semilunar valves (Fig. 52, V.A.V.), lying in the transverse dorso-lateral plane. The efficiency of these valves was demonstrated when the arterial system was injected. The injection was made into the efferent vessel of the left branchia, and thus reached the ventricle *via* the left auricle. In no case did it flow into the right auricle, except in quite negligible quantities.

The ventricle (VE.) is bent at roughly a right angle, one arm pointing anteriorly and the other to the left. The right auricle opens into it at the outside of the angle, and the left at the end of the laterally placed arm of the angle. The ventricle has a thick spongy wall, the inside of which is composed of a loose network of interlaced muscular fibres.

The following arteries leave the ventricle :

(*a*) Cephalic artery.
(*b*) Posterior aorta.
(*c*) Genital artery.
(*d*) Anterior renal artery.

The exits of the cephalic artery (CE.A.) and the posterior aorta (P.AO.) are each guarded by a single semilunar valve (V.C.A. and V.P.A.). Each of these valves is attached to the dorsal wall of the heart. The cephalic artery departs from the end of the anterior arm of the ventricle, and the posterior aorta from the posterior surface of the lateral arm. The genital artery (G.A.) leaves the anterior surface of the ventricle from the apex of the angle. The anterior renal artery (A.R.A.) which is very small, departs from a point close to the genital artery, a little to the right. The exits of these arteries are not guarded by valves, but the openings from the ventricle into them are small and slit-like, so that they may be closed during diastole.

(*a*) CEPHALIC ARTERY. (Figs. 47, 49, 58, CE.A.)

This is the largest artery in the body. It leaves the anterior end of the heart as a stout trunk, which bends a little to the left and then runs straight forward immediately dorsal to the oesophagus. Just before it reaches the cephalic cartilage it forks into two branches (Fig. 58, unlettered), which are often of unequal calibre. These branches pass between the visceral and pedal ganglia

(Figs. 47, 49, 58.) and reunite on the ventral side of the brain in the middle line, to form the anterior cephalic artery (Figs. 47, 49, A.C.A.). This artery runs forward immediately ventral to the brain. Just anterior to the brachial ganglion it forks into two branches which run round the inner surface of the buccal sinus to their termination in the dorsal part of the head muscles.

The following paired and other branches are given off from the cephalic artery:

1. Ventral gastric artery. (Fig. 47, V.G.A.).

This leaves the cephalic artery close to the ventricle, and supplies the posterior part of the oesophagus (P.O.A.), the ventral part of the stomach (ST.), part of the intestine (IN.), the caecum (CA.) and part of the left and right pancreas.

2. Anterior accessory genital artery. (Fig. 47, A.G.A.).

This artery either leaves the cephalic artery close to the ventral gastric artery or else it is given off from the beginning of the latter. It supplies the anterior part of the genital duct, also sending branches to the anterior walls of the renal chamber and to the anterior renal appendages.

3. Dorsal gastric artery. (Fig. 47, D.G.A.).

This artery is usually given off a little anterior to the ventral gastric artery. It is rather smaller than the latter and less extensive in its distribution. It supplies the dorsal surface of the stomach, and part of the left pancreas.

4. Ventral shell sac artery. (Fig. 47, V.S.A.).

This is a median artery which is given off from the dorsal wall of the cephalic artery. It sends branches all over the ventral wall of the shell sac.

5. Anterior mantle arteries. (Fig. 47, A.M.A.).

These are very large paired arteries. They are given off together and each runs outwards and forwards just dorsal to the liver. If the latter is removed these arteries are exposed. Almost immediately after they leave the cephalic artery each of the anterior mantle arteries gives off a hepatic artery (H.A.). This constitutes the entire arterial supply of each digestive gland. Each of the anterior mantle arteries also sends branches to the outer collar muscle of the funnel (O.C.A.), to the posterior part of the retractor muscles of the head (R.H.A.), the retractor muscles of the funnel (R.F.A.), three or more large branches (B.A.M.A.) to the muscular walls of the mantle, and a large branch (A.F.A.) to the anterior part of the fin. This last passes through the mantle wall close to the nerve which innervates the fin muscle.

6 and 7. Anterior oesophageal arteries and arteries of posterior salivary glands. (Fig. 47.).

The anterior oesophageal arteries (A.O.A.) are given off just before the cephalic artery forks. They run posteriorly, and also supply part of the posterior salivary glands (P.S.G.). The arteries of the posterior salivary glands are a pair of very small arteries (Fig. 47, unlettered) which are given off a little way anterior to the forking of the cephalic artery.

8. Posterior funnel arteries. (Figs. 47, 49, 58, P.FU.A.).

These are large arteries given off a little before the two forks of the cephalic artery enter the skull (Fig. 58, P.FU.A.). They join the posterior funnel nerves and run beside them, passing to the ventral side of the body, and then postero-laterally to their final distribution in the posterior part of

the funnel. Branches of these arteries supply the retractor muscles of the head and the dorsal wall of the shell sac.

9. Buccal arteries. (Figs. 47, 49, 57, 58, B.A.).

These are given off at the same point as the posterior funnel arteries. They are large vessels which immediately enter the peri-oesophageal sinus which passes through the brain, and run forward, one on either side of the oesophagus, lying freely in the sinus. They enter the buccal mass on the postero-ventral side of the latter, and divide into several branches, which are distributed throughout the whole of the buccal mass.

10. Ophthalmic arteries. (Fig. 29, 47, 49, 58, 60, O.A.).

These are given off from the forks of the cephalic artery. They run laterally dorsal to the optic nerves attached to the superior anterior ophthalmic nerves (Fig. 29, O.A.), and on reaching the eyeball fork into two, one branch going to the iris (Fig. 60, IR.A.), round the base of which it forms a ring, and the other to the retina. These branches give off numerous small branches to the white body and the oculomotor muscles. In addition a small branch (Fig. 47, D.O.A.) is given off soon after each main ophthalmic artery leaves the cephalic artery. This is the dorsal orbital artery, which passes through the orbital cartilage and supplies the posterior and dorsal parts of the orbit.

11. Anterior funnel arteries. (Figs. 47, 49, A.FU.A.).

These are smaller than the posterior funnel arteries. They are given off where the two forks of the cephalic artery re-unite on the ventral side of the brain to form the anterior cephalic artery (Fig. 47, A.C.A.). They pass through the skull with the anterior funnel nerves and

then run alongside and a little posterior to the anterior funnel nerves and supply the anterior part of the funnel. They also send small branches to the anterior ventral part of the retractor muscles of the head.

In addition to the arteries already described several small arteries are given off in the head region, supplying the optic ganglia and the ganglia of the brain. These have not been figured. The artery to the optic ganglion is given off from the fork of the cephalic artery immediately anterior to the origin of the ophthalmic artery, and passes through the centre of the optic nerve to the optic ganglion. Just before the two forks of the cephalic artery unite to form the anterior cephalic artery, two small branches are given off to the visceral and pedal ganglia respectively. A small artery enters the brachial ganglion from the anterior cephalic artery.

12. Ventral orbital arteries. (Fig. 47, V.O.A.).

These are fairly large arteries which are given off just after the anterior cephalic arteries have forked. They supply the ventral walls of the orbit.

13 and 14. Tentacle arteries (Figs. 47, 51, T.A.) and brachial arteries (Figs. 47, 50, BR.A.).

These are given off from the forks of the anterior cephalic artery. They run along the centres of the arms and tentacles respectively, next to the main nerves, just aboral to them.

15. Dorsal head arteries. (Fig. 47, HE.A.)

These consist of several arteries which supply the dorsal part of the head posterior to the arms. They are given off at roughly the same points as are the brachial arteries, but run posteriorly.

(*b*) POSTERIOR AORTA. (Figs. 20, 47, P.AO.)

This, like the cephalic artery, is a very stout trunk. It leaves the ventricle from the posterior surface of the latter and after travelling a short distance posteriorly, comes to the ventral surface of the visceral dome close to the left-hand border of the inksac (Fig. 5, P.AO.) in the region where the wide vesicle of the latter narrows into the more slender duct. It divides into the right and left posterior mantle arteries (Figs. 5, 20, 47, P.M.A.), which run transversely across the posterior part of the visceral dome, covered only by the skin of the latter.

The following branches are given off :

1. Ink gland artery. (Figs. 20, 47, IS.A.)

This is quite a large artery which is given off almost immediately after the posterior aorta leaves the ventricle. It runs first slightly forwards and then posteriorly ; it passes through the dorsal wall of the inksac and enters the ink gland. This artery gives off two branches just after leaving the posterior aorta. The largest of these, the intestinal artery (I.A.) supplies part of the intestine, the left renal appendages, and the left branchial heart. The other, the posterior renal artery (P.R.A.) supplies the posterior part of the right renal appendages and the right branchial heart.

2. Rectal artery (R.A.).

This is quite a small artery, which leaves the posterior aorta shortly before the latter forks, and runs anteriorly between the duct of the inksac and the rectum, both of which it supplies.

3. Posterior mantle arteries.
(Figs. 20, 47, P.M.A.)

These are large paired arteries formed by the forking of the posterior aorta. They run transversely over the ventral surface of the posterior part of the visceral dome

to the walls of the mantle. Two unpaired branches are given off from these arteries. One of these is the median mantle artery (Fig. 47, M.M.A.) which runs along the anterior edge of the mesial membrane dividing the posterior part of the mantle cavity into two, and then forwards along the mid-ventral line of the mantle wall which it supplies. The other is the siphuncle artery (S.A.) which runs posteriorly over the ventral surface of the visceral dome to the posterior apex of the animal. In the male this sometimes gives off small branches to the testis. The exact origin of both these arteries varies considerably. The left posterior mantle artery also gives off a small branch, the posterior accessory genital artery (P.G.A.), which supplies the posterior part of the genital duct.

The main part of each posterior mantle artery divides into several branches just before it enters the mantle wall. One of these (P.F.A.) supplies the posterior part of the fin muscle and the others (B.P.M.A.), the posterior part of the mantle wall and the posterior part of the dorsal wall of the shell sac. The posterior mantle arteries also give off several small branches which have not been mentioned. These travel over the ventral surface of the visceral dome, supplying the skin and the walls of the inksac. In the female small branches supply the nidamental glands.

(*c*) GENITAL ARTERY. (Fig. 21, G.A.V., Figs. 47, 52, G.A.)

This artery leaves the heart from the inside of the apex of the angle of the ventricle (Fig. 52, G.A.). It runs dorsal to the heart straight back to the gonad (Fig. 21, TE.). Throughout its course it is attached to the dorsal wall of the viscero-pericardial coelom. It usually gives off only very minute branches to the membrane to which it is attached.

(*d*) ANTERIOR RENAL ARTERY. (Figs. 47, 52, A.R.A.)

This is a very small artery which supplies the anterior part of the renal appendages. It leaves the heart close to the genital artery, but slightly to the right of it, and immediately divides into several branches.

B. Venous System.

[DISSECTION.—*Injection is essential for satisfactory dissection.* (*See page* 149 *for practical instructions.*) *Most of the veins are comparatively superficial, and are exposed when the skin is removed and the body cavities opened. But to follow the two azygos veins it is necessary to remove one of the digestive glands. To investigate the sinuses of the head make a lateral dissection of the head region.*]

The venous system has been treated under the following headings:

(*a*) Cephalic vein (and factors).
(*b*) Sinuses of head.
(*c*) Venae cavae (and factors).

(*a*) CEPHALIC VEIN. (Figs. 5, 20, 48, 49, CE.V.).

This vein runs down the mid-ventral line of the anterior part of the body. It is formed anteriorly by the ring vein (Fig. 48, R.V.H.) of the head, which runs round the oral side of the bases of the arms where the buccal funnel is joined to the latter. At the point where the bases of the two ventral arms unite, the ring vein opens into a median longitudinal vein (Figs. 23, 48, A.C.V.) which has been called the anterior cephalic vein to distinguish it from the rest of the cephalic vein.

The anterior cephalic vein is a thin-walled vessel, which runs straight back and passes dorsal to the funnel. At a point just ventral to the anterior end of the statocyst cartilage it passes through paired semilunar valves

(Fig. 48, unlettered) into a large muscular chamber (Figs. 23, 48, M.CE.V.) which constitutes the anterior part of the main cephalic vein (Fig. 48, CE.V.). The muscular chamber lies immediately dorsal to the exhalent tube of the funnel. The anterior part of its walls are attached on the dorsal side to the diaphragm cartilage, (Fig. 23, D.CA.) which lies just dorsal to the chamber. A peculiarity of the structure of this chamber is a little unpaired tie-bar (Fig. 48, T.B.) situated somewhat on the right side and extending from the dorsal to the ventral wall.

The openings of all the main factors which enter the cephalic vein are guarded by valves. Powerful peristaltic waves pass posteriorly along this vein in life, driving the blood from the head region in the direction of the venae cavae (V.C.). The cephalic vein extends posteriorly to a point about in line with the renal papillae (Fig. 20, RE.P.).

The following paired and other factors enter the cephalic vein (with which are included the ring vein and the anterior cephalic vein) :—

1. Brachial and tentacle veins. (Figs. 48, 50, 51).

Each arm is drained by four main veins, one running along the middle of the oral surface (Fig. 50, BR.V.), one at each side of the oral surface (L.B.V.), and one along the middle aboral line (A.V.A.). The three vessels on the oral side of the arm return blood directly to the ring vein (Fig. 48, R.V.H.), while in all except the ventral arms, the aboral vessels open into the dorsal head vein (D.H.V.), which in turn opens into the ring vein. In the case of the ventral arms the aboral vessel opens into the ventral head vein (V.H.V.). Each tentacle is drained by a large vein (Fig. 51, T.V.) running along its oral surface. This vein opens into the dorsal head vein (Fig. 48, D.H.V.).

2. Dorsal head veins. (Fig. 48, D.H.V.).

In addition to the factors which enter them from the

arms and tentacles, these veins receive factors from the postero-dorsal surface of the head and from the orbit. They open into the ring vein.

3. Veins of peri-buccal sinus. (Fig. 48, V.R.S.).

These are very short paired laterally situated veins, which, shortly after leaving the ring vessel, open into the peri-buccal sinus (P.B.S.) a short way from the anterior limit of the latter. The openings are guarded by simple valves, the structure of which indicates that the blood passes chiefly from the ring vessels into the sinus, and that flow in the opposite direction is restricted. This is borne out when the venous system is injected from the peri-buccal sinus, though the injection will to some extent pass into these veins.

In addition to the veins mentioned there are numerous other small vessels which open into the ring vein, including veins which link the latter with the dorsal head veins. There is a great deal of anastomosing among the veins of the head.

4. Ventral head veins. (Fig. 48, V.H.V.).

These veins return blood from the aboral side of the ventral arms and from the ventral walls of the tentacle pockets (Fig. 25, T.PO.) They open into the anterior cephalic vein (Fig. 48, A.C.V.).

5. Sinus veins. (Fig. 48, SI.V.).

These veins run from the peri-oesophageal sinus (Fig. 36, O.S.V.), and after travelling lateral to the brachial and pedal ganglia, they pass through large foramina (Figs. 27, 28, F.O.V.) in the skull. Each of these veins is in communication (Fig. 48, C.O.S.) with the corresponding optic sinus (O.S.). The right sinus vein usually opens into the anterior cephalic vein (A.C.V.) just anterior to the paired semilunar valves through which the latter enters the cephalic vein. The left sinus vein, on the other hand,

opens directly into the muscular chamber (M.CE.V.) of the cephalic vein through paired semilunar valves (Fig. 48, unlettered) but sometimes the relative position of the openings of these two veins is reversed. Just before each of the sinus veins joins the main venous trunk, it receives a factor (T.P.V.) from the tentacle pocket and the anterior part of the retractor muscles of the head.

6. Ophthalmic veins. (Fig. 48, O.V.).

These veins travel posteriorly from the optic sinuses (Figs. 48, 67, O.S.), passing through foramina (Figs. 27, 28, F.V.E.) of the skull. They are slender veins but their openings into the muscular chamber of the cephalic vein are large and thick-walled. Just before they enter the cephalic vein they also receive small factors (Fig. 48, unlettered) from the anterior part of the retractor muscles of the head.

7. Anterior funnel veins. (Fig. 48, A.F.V.).

These are large veins which receive blood from most of the funnel, including the exhalent tube, and the inner and outer collar muscles. They enter the muscular chamber of the cephalic vein immediately posterior to the ophthalmic veins. These veins are guarded by simple valves.

8. Ventral funnel veins.

These are several quite small paired veins (not figured) which return blood from the anterior part of the exhalent tube of the funnel. They open into the ventral wall of the muscular chamber (Figs. 23, 48, M.CE.V.).

9. Anterior azygos vein. (Fig. 48, V.A.A.V., Fig. 49, A.A.V.).

This is an important vein which opens into the mid-dorsal wall of the muscular chamber through a single semilunar valve. It is made up of numerous factors, the chief of which are :—

(*i*) Pallial veins (Fig. 49, unlettered) which come from

the region of the stellate ganglia, where they receive factors from the mantle walls. They run along beside the pallial nerves (P.N.), receiving during their course factors from the inner and outer collar muscles, and from the shell sac.

(*ii*) Factors from dorsal part of retractor muscles of head.

(*iii*) Factors from posterior salivary glands (P.S.G.).

(*iv*) Anterior oesophageal vein (Fig. 49, unlettered), which is a median vessel running along the ventral surface of the oesophagus, and returns blood from the region of the oesophagus which lies between the anterior part of the liver lobes.

(*v*) Anterior hepatic veins (Fig. 49, unlettered), from the anterior part of the liver.

(*vi*) Small factors (not figured), which follow the course of the visceral nerves (V.N.) through the liver, and return blood from the ventral part of the sheath enclosing the latter.

The main median part of this vein which is shown together with its principal factors in Figure 49 (A.A.V.), runs from immediately ventral to the oesophagus to the cephalic vein, passing either to the left or the right of the paired visceral nerves (V.N.) which lie close together. It also communicates with the posterior end of the peri-oesophageal sinus, by a small vessel which leaves the extreme posterior end of the latter, usually at a point just lateral to where the duct of the right posterior salivary gland enters the sinus. This communication has not been figured. It can be seen if the peri-oesophageal sinus is opened from the dorsal side.

10. Posterior funnel veins. (Figs. 6, 48, P.F.V.).

These large paired veins are composed of two main factors, which drain the anterior parts of the retractor muscles of the funnel and head respectively. There is

usually a marked difference in the region of junction of these two factors in the left and right veins.

11. Posterior azygos vein. (Fig. 48, V.P.A.V., Fig. 49, P.A.V.).

This, like the anterior azygos vein, is a large median vessel. It opens through a semilunar valve into the dorsal wall of the cephalic vein, a little anterior to where the latter forks into the two venae cavae. The only part of this vein to which the name azygos can be applied is the actual opening of the vein into the cephalic vein, and the vestibule next to this opening, which receives numerous factors.

These are :—

(*i*) Paired posterior veins from the retractor muscles of the head and funnel (Fig. 48, P.V.R.M., Fig. 49, unlettered), which run over the ventral surface of the liver, each receiving a factor from the posterior part of the liver.

(*ii*) Paired median hepatic veins (Figs. 48, 49, M.H.V.) which return blood from the middle part of the liver, and are the largest of the veins which drain it.

(*iii*) Anterior pancreatic veins (Fig. 48, A.P.V., Fig. 49, unlettered), which return blood from the anterior part of the pancreatic appendages.

(*iv*) Median oesophageal vein (Fig. 49, unlettered), returning blood from the region of the oesophagus which runs between the posterior part of the lobes of the liver.

(*v*) Median shell sac vein (Fig. 49, M.S.V.), which receives factors from the ventral wall of the shell sac, and also from the dorsal wall of the renal sac, and opens into the azygos vein after travelling to the left of the oesophagus (OES.).

(*b*) SINUSES OF THE HEAD.

There are four blood sinuses in the head :—

1. Peri-buccal sinus.
2. Peri-oesophageal sinus.

3 and 4. Paired optic sinuses.

1. Peri-buccal sinus. (Figs. 36, 48, 49, P.B.S.).

This is a large hollow formed by the united bases of the arms. It is shaped like the inside of an egg-cup, into which the buccal mass (Fig. 36, B.M.) fits like an egg. A large pair of veins (Fig. 48, V.R.S.) opens into it from the ring vein (R.V.H.), which drains the arms. They open laterally a short distance from the anterior limit of the sinus. In addition one or more pairs of smaller veins open into it from the ring vein, and numerous small veins from the anterior end of the buccal mass. These latter drain the lips and the anterior part of the jaw muscles.

Postero-ventrally a membranous flap of tissue is loosely fastened to the wall of this sinus (Fig. 49, unlettered). Blood can pass between this flap and the wall of the sinus, and thence pass posteriorly into the sinus vein (Fig. 49, O.S.V.).

2. Peri-oesophageal sinus. (Figs. 36, 48, 49, P.O.S.).

The anterior limit of this sinus is about two-thirds of the length of the buccal mass from its anterior end. The anterior part of the peri-oesophageal sinus lies within the peri-buccal sinus, from which it is separated by a delicate membrane, reinforced, except on the ventral side, by the retractor muscles (Fig. 36, L.M.B. and O.M.B.) of the buccal mass. Near the posterior limit of the peri-buccal sinus, the latter communicates with the peri-oesophageal sinus by paired foramina (Figs. 36, 48, 49, F.O.B.). These are large oval apertures situated ventro-laterally in the separating membrane. The anterior part of this sinus receives several veins from the muscles of the buccal mass, which enter it at its anterior limit. In addition a median vein (Fig. 49, unlettered) opens into it immediately dorsal to the duct (D.S.G.) of the posterior salivary glands. This drains the more centrally situated parts of the buccal mass.

On either side of the superior buccal ganglion (S.B.G.) there are paired apertures (not figured) belonging to veins from the neighbourhood of the former. These veins form a small sinus-like sac immediately dorsal to the ganglion, which receives factors from the neighbouring tissues.

The peri-oesophageal sinus extends back to the posterior limit of the skull. It passes through the centre of the brain (Fig. 49), and the oesophagus (OES.), the paired buccal arteries (B.A.) and the median duct (D.S.G.) of the posterior salivary glands (P.S.G.), formed by the uniting of the ducts of the paired glands just after they enter the sinus, lie freely in it. Several small veins open into the posterior part of the sinus. These come from the brain and the posterior salivary glands.

The exits of the peri-oesophageal sinus are paired perforations of its walls (Figs. 36, 49, O.S.V.), lying laterally a little posterior to the foramina (F.O.B.) communicating with the peri-buccal sinus. They lead into the paired sinus veins (Fig. 48, SI.V.) which run postero-ventrally on either side of the brachial and pedal ganglia, and open, as previously mentioned (page 87) into the cephalic vein. In addition there is a small communication from the posterior end of this sinus to the anterior azygos vein.

3. Optic sinuses. (Figs. 48, 67, O.S.).

These sinuses lie mesial to the eyeballs and enclose the white bodies which surround the optic ganglia. They receive several veins draining the various parts of the eyes. These veins include an annular vein which drains the iris, and closely follows the course of the corresponding artery. Postero-ventrally the ophthalmic veins (Fig. 48, O.V.) pass from the optic sinuses through the orbital cartilages and open into the muscular chamber of the cephalic vein. In addition these sinuses communicate with the sinus veins (Fig. 48, C.O.S.).

(*c*) VENAE CAVAE. (Figs. 20, 48, V.C.).

These are formed by the forking of the cephalic vein (CE.V.) posterior to the renal papillae (Fig. 20, RE.P.). They lie in the ventral renal chambers (V.CH.) of the renal sac, attached to the dorsal walls of the latter. They are covered with branching glandular renal appendages (Figs. 20, 48, RE.A.). These are hollow and their cavities open into the venae cavae. These appendages not only cover the venae cavae, but all the veins which lie in the ventral renal chambers. The venae cavae receive the following factors :—

1. Mesenteric veins. (Figs. 20, 48, L.M.V. and R.M.V.).

These are large veins which open into the anterior part of the venae cavae. The left mesenteric vein follows the course of the duct of the left digestive gland, and receives factors from the dorsal and ventral walls of the caecum, from the intestine, the dorsal wall of the stomach, and from the left pancreas. The right vein, called the genito-mesenteric vein (see page 35) lies in the middle line close to the genital artery (Fig. 21, G.A.V.). It returns blood from the gonad, the caecum, the ventral walls of the stomach, and from the right pancreas. It also receives a small factor from the wall of the ventricle.

2. Inksac vein. (Figs. 20, 48, IS.V.).

This is a large vein which leaves the dorsal wall of the inksac and runs anteriorly to enter the right vena cava. Just before it enters the ventral renal chamber (Fig. 20, V.CH.) it expands into a small sinus. It drains blood chiefly from the ink gland, but receives small factors from the wall of the inksac as well.

3. Intestinal vein.

This is shown but not lettered in Figures 20 and 48. It is a small vein which returns blood from the ventral part of the loop of the intestine, and enters the left vena cava at

a point corresponding to the place where the inksac vein (IS.V.) enters the right vena cava.

4. Cardiac veins.

The right vena cava also receives two or more small veins from the wall of the ventricle. (These have not been figured.)

5. Anterior mantle veins. (Figs. 5, 20, 48, (A.M.V.).

These are large veins which enter the venae cavae (Figs. 20, 48, V.C.) where the latter open into the branchial hearts (B.H.). They each receive the following factors :—

(i) Three or more large factors (Figs. 20, 48, F.A.M.V.) from the mantle wall.

(ii) Anterior fin vein (Figs. 20, 31, 48, A.FI.V.), which is composed of numerous factors which run beside the nerves to the fin, and unite into a single large vein (Fig. 48, A.FI.V.) a short way posterior to the stellate ganglion (S.G.). This vein runs posteriorly just lateral to the retractor muscle of the funnel. It also receives anteriorly a factor (Fig. 48, unlettered) from the region of the stellate ganglion, which drains the anterior region of the mantle.

(iii) Posterior shell sac vein (Fig. 48, P.S.V.). This originates in the posterior part of the ventral wall of the shell sac, but also receives several factors from the posterior parts of the retractor muscles of the head and funnel, in the region of their origin.

(iv) Branchial gland vein (Figs. 20, 48, 54, V.B.G.). This vein runs along the dorsal edge of the branchial gland (Fig. 54, B.GL.) which it drains.

(v) Branchial muscle vein (Fig. 54, V.B.M.). This is a small vein, not shown in Figure 48, which runs along the axis of the branchia, a little dorsal to the afferent branchial vessel (Fig. 54, A.V.) and close to the branchial nerve (Fig. 54, unlettered).

In addition to the above-mentioned paired veins, the

left anterior mantle vein receives the anterior accessory genital vein (Fig. 48, A.G.V.). This opens into the left anterior mantle vein (A.M.V.) just before the latter joins the vena cava (V.C.). In the female it is a small vein, which drains the anterior part of the genital duct. It is larger in the male, owing to the greater size of the male genital duct.

The main trunk of each anterior mantle vein formed by the various factors, enlarges into a thin-walled sinus before entering the ventral renal chamber.

6. Posterior mantle veins. (Figs. 5, 20, 48, P.M.V.).

These are composed of several large factors (unlettered in Fig. 48) from the posterior part of the mantle wall, and of the posterior fin veins (Figs. 31, 48, P.FI.V.), which drain the posterior part of the swimming muscles of the fins. After these factors have united, the posterior mantle veins enlarge into thin-walled sinuses, lying on the posterior ventral surface of the visceral dome. They enter the ventral renal chambers (Fig. 20, V.CH.), and after travelling anteriorly for a short distance, open into the venae cavae (V.C.) close to where the latter open into the branchial hearts (B.H.).

In addition to the paired factors of the posterior mantle veins which have already been mentioned, there are several unpaired factors corresponding to similar branches of the posterior mantle arteries. These veins, all of which enter the sinus of the left posterior mantle vein, consist of the following :—

(i) Median mantle vein (Fig. 5, M.A.V. ; Fig. 48, M.M.V.), which runs beside the median mantle artery. It drains the median ventral part of the mantle wall, and passes to the visceral dome along the anterior edge of the membrane which divides the posterior part of the mantle cavity into two.

(ii) A small rectal vein (not figured) from the rectum and duct of the inksac, which enters the left posterior mantle vein close to the median mantle vein, or else joins the median mantle vein before the latter enters the posterior mantle vein.

(iii) Posterior accessory genital vein (Fig. 48, P.G.V.), which drains the posterior part of the genital duct.

(iv) Siphuncle vein (Figs. 6, 48, S.V.), which comes from the posterior apex of the animal, passing ventrally to the inksac, and which in the male sometimes receives small factors from the testis (Fig. 48, TE.).

Various other small veins open into the posterior mantle veins, just before the latter enter the renal sac. These come from the wall of the inksac, the skin of the visceral dome, etc. In the female they include veins from the nidamental glands.

Unless the injection has filled them, many of the veins described may be easily overlooked, owing to the extreme thinness of their walls, even though the vessels themselves may be comparatively large.

C. Branchial Circulation.

On each side of the body three great veins, the vena cava (Fig. 48, V.C.), the anterior mantle vein (A.M.V.) and the posterior mantle vein (P.M.V.) all converge to the opening (Fig. 54, O.V.C.) into the corresponding branchial heart. These three veins drain the venous blood from every region of the body. The opening into the branchial heart (B.H.) is guarded by a pair of semilunar valves, shown but not lettered in Figure 48.

The branchial heart itself is shown in section in Figure 48. It has thick spongy walls, into which the blood can penetrate. It drives the blood by rhythmical contractions into the afferent branchial vessel (Fig. 54, A.V.). This vessel lies centrally within the branchia immediately

ventral to the axial part of the retractor muscle of the branchia (A.R.B.), which forms the main structural support of the branchia. According to Bert (1867) the two branchial hearts contract simultaneously, the rate of heart-beat being about 40 to the minute under average conditions when the animal is at rest.

Back flow into the branchial heart is prevented by six little fleshy valves in the afferent vessel, situated a short way from the heart. These are shown but not lettered in Figure 48. They were mentioned by Cuvier (1817), who states that similar valves are not present in *Octopus*, but they are not mentioned anywhere else in the literature.

The branchia has a pinnate structure and the main afferent branchial vessel gives off branches to each of the branchial laminae. The blood flows from these branches into the capillaries of the delicately folded respiratory filament (Figs. 53, 54, R.F.B.). Capillaries from the latter enter the factors of the efferent branchial vessel which runs along the ventral edge of each of the laminae. The main efferent vessel (E.V.) lies along the mid-ventral line of the branchia, just dorsal to the marginal part (Fig. 54, M.R.B.) of the branchial muscle. Posteriorly it widens out into the auricle (AU.).

The afferent branchial vessel also gives off small branches to the branchial gland (B.GL.), which thus appears to be supplied with venous blood. Each of the vessels which supply the branchial gland passes along the thin membrane (M.R.F.) which helps to hold the respiratory filament in place. It is possible that the walls of these vessels may be sufficiently thin for gaseous interchange to take place directly. One of these vessels is shown but not lettered on the right hand side of Figure 54.

RESPIRATORY SYSTEM.

A. STRUCTURE OF BRANCHIAE (see page 54).

B. STRUCTURE OF RESPIRATORY FILAMENTS (Figs. 53, 54, R.F.B.).

As previously stated each branchia has a pinnate structure with numerous laminae projecting on either side of a central axis. Each of these laminae bears a section of respiratory filament, which stretches between the corresponding branch and factor of the afferent and efferent vessels respectively. This membrane has a very delicate structure and is thrown into fine folds lying at right-angles to the main blood vessels of the lamina. These folds are themselves transversely plicated, so that the whole branchia has a tripinnate structure (Fig. 53). In this way the area of the respiratory surface is greatly increased. The folds are quite small and delicate. In preserved specimens which have been kept for some time, and in fresh specimens which have come on a journey, the branchiae may be so damaged that the folds cannot be seen.

C. BRANCHIAL CIRCULATION.

This has already been described (page 96).

D. CIRCULATION OF WATER OF RESPIRATION.

Even when the animal is at rest the muscular mantle is continuously drawing water into the mantle cavity and forcing it out, by rhythmically increasing and diminishing the capacity of the cavity. The water enters it at the sides of the neck (Fig. 24, I.SI.), between the lateral valves (L.P.) of the funnel and the mantle wall (M.M.). A valve (Fig. 6, F.V.) within the exhalent tube (Fig. 24, E.S.F.) of the funnel prevents water from entering this way. In exhalation it is forced out through the exhalent tube of the funnel. The lateral valves of the funnel are extended by

the pressure of the water on the inside of their walls, which prevents it from escaping the way it entered. The circulation of water within the mantle cavity is thus so arranged that there is little chance of faecal matter from the anus and renal papillae being forced against the delicate respiratory filaments, while at the same time these waste products are expelled from the mantle in the stream of exhaled water. According to Bert (1867) the rate of respiration under average conditions when the animal is at rest is about 55 inspirations per minute.

EXCRETORY SYSTEM.

The RENAL SAC has already been described in detail (pages 30 *et seq.*). It consists of paired ventral chambers in which run several veins, all of which are covered with voluminous venous appendages, and of a dorsal chamber in which float the so-called pancreatic appendages which hang from the ducts of the digestive glands. All three chambers are intercommunicating, and open to the exterior by means of paired renal papillae, lying on either side of the rectum.

The VENOUS APPENDAGES (Fig. 20, RE.A. and Text-Fig. 5, unlettered) are hollow and branching, their cavities being continuous with the veins from which they hang. They are covered with a glandular epithelium which is excretory in function. They extract waste products from the blood and pass them into the renal sac.

The PANCREATIC APPENDAGES (Fig. 21, PA.) have a structure rather similar to that of the appendages of the veins. They are hollow and branching and their cavities are continuous with the ducts (D.L.) of the digestive glands. They have a very rich blood supply. According to Castaldi and Musio (1928) these appendages are also partly excretory in function, as they are stated to have two layers of cells, an inner secretory one, secreting into the hepatic duct, and an outer excretory, excreting into the renal sac.

NERVOUS SYSTEM.

The first detailed description of the nervous system of *Sepia officinalis* was published by Chéron (1866) in his "Recherches pour servir à l'histoire du système nerveux des Céphalopodes dibranchiaux," in which he included good descriptions of the nervous system of *Eledone moschata*, *Octopus vulgaris* and *Sepia officinalis*.

Hillig (1912) in a work entitled "Das Nervensystem von Sepia officinalis L.", gives a clear and detailed account of the nervous system of *Sepia*, which is supplemented by very fine figures. A certain amount of comparative work is also included, and there is an extensive bibliography. In spite of its general excellence this account contains one obvious error, which is, however, almost certainly a slip of the pen. Hillig describes an inferior anterior ophthalmic nerve, which, he says, after travelling in the muscular anterior wall of the orbit from the brachial ganglion, innervates the iris. This is impossible, as there is no connection on this side between the eyeball, to which the iris is attached, and the anterior wall of the orbit. This nerve goes in fact to the eyelid.

Similarly he describes the inferior posterior ophthalmic nerve as innervating the region of the iris. Hillig's criticism of the drawings of most of the earlier authors indicates that he attached great importance to correct proportions in anatomical figures, and his own figures are very exact in this respect. One can therefore say with confidence that in his Plate XXXIV, Figure 9, which shows both the inferior anterior, and the inferior posterior ophthalmic nerves, these nerves travel laterally so much further than the superior anterior and the superior posterior ophthalmic nerves, that they must be innervating the eyelid and not the iris. It is thus evident from this figure that Hillig's dissection was quite correct, and that it is only in the text that this slip occurs.

Hillig made a very thorough study of the literature, and in addition to discovering several new nerves, he renamed many of them. Although he expresses the desire that, especially in the case of the nerves of the eye, his names should not be accepted as final, but are only intended to serve until physiological investigation has established more definitely the nature and full distribution of these nerves, in the absence of such further investigation Hillig's nomenclature has been adopted here for all the nerves, using the English translation of his Latin names. For a more detailed account of the nervous system than it is possible to give here, the reader is referred to this work by Hillig.

The nervous system of *Sepia*, as of all Dibranchiates, is highly organised. The main ganglia are very large, and concentrated in the head region into a solid mass of nervous tissue. Only slight traces remain of their originally paired condition, and they have become so much fused that the resultant nervous mass can be referred to as the brain.

The brain is composed of four large ganglion masses, the cerebral ganglion (Figs. 56, 57, 79, C.) lying dorsally, and the visceral (Figs. 56, 57, 58, 79, V.G.), pedal (Figs. 56, 58, 79, P.) and brachial ganglia (BR.G.) lying ventral to it. The cerebral ganglion is joined to the rest of the brain by a pair of very stout commissures (Fig. 58, C.L.C.) lying on either side of the peri-oesophageal blood sinus (Fig. 57, P.O.S.) which passes through the brain. In addition there is a much smaller ganglion, the superior buccal ganglion (Figs. 56, 57, 79, S.B.G.), lying anterior to the cerebral ganglion and connected to the cerebral and brachial ganglia only by slender commissures. When the isolated brain is viewed from the side (Fig. 56), no sharp separation of the main ganglia is seen, but in sagittal section the separation is quite distinct (Fig. 79).

The brain is partly enclosed by the cartilaginous skull

(see Fig. 79) and where this is lacking it is bounded by a tough membrane. A large number of quite distinct nerves are given off, which show but little variation in individual specimens. The largest nerves have ganglia on their courses. The extremely stout optic nerves (Fig. 57, C.O.N.) swell out into kidney-shaped optic ganglia (OP.G.), which lie on either side of the brain, and together are nearly as big as the brain itself. Individual bundles of retinal nerves (RE.N.) are given off from each of these ganglia, and enter the retina separately. Lying on the dorsal side of the optic nerves close to the cerebral ganglia are the small olfactory ganglia (Fig. 57, O.G.). The pallial nerves swell up into large stellate ganglia (Fig. 55, S.G.), after running some distance from the brain. The visceral nerves exhibit small ganglia (Figs. 54, 55, B.GA.) at the bases of the branchiae. Each of the branchial nerves (Fig. 56, B.N. 1–4) swells up into a small ganglion (Fig. 56, unlettered) just before it enters the main part of the arm.

The central nervous system co-ordinates and controls most of the bodily functions, including swimming, colour changes and heart beat.

In addition to the central nervous system, or brain, and the peripheral nervous system, composed of the nerves radiating from the brain, there is a sympathetic system. This consists of two ganglia, the inferior buccal ganglion (Figs. 36, 49, I.B.G.), lying on the postero-ventral surface of the buccal mass, and connected to the superior buccal ganglion (Fig. 49, S.B.G.) of the central nervous system by a pair of slender commissures (C.B.S.), passing on either side of the oesophagus; and the gastric ganglion (Figs. 36, 55, G.G.) lying on the anterior ventral surface of the stomach. These two ganglia are connected by a pair of sympathetic nerves (Fig. 36, S.N.) which lie against the wall of the oesophagus. They give off numerous nerves to the various parts of the digestive system.

An interesting piece of work has been done by Sereni (1929) which gives an idea of the complexity of function of the central nervous system of Cephalopods. This work deals with the control of the chromatophores. According to Sereni there are motor centres in the inferior oesophageal ganglion, a general colouration centre, probably located in the pedal ganglion, which overrules the former, and an inhibitory centre in the cerebral ganglion. Sereni says that the delicacy of control of the chromatophores has been achieved by the combination of two types of control, excitatory and inhibitory.

A. Central Nervous System.

[DISSECTION.—*The dissection of the central nervous system should be commenced from the dorsal side. Place the animal on its ventral side and remove the shell. At the apex of the nuchal cartilage* (Fig. 79, N.C.) *expose the cephalic cartilage by removing the muscles which cover it. When this cartilage is dissected away the cerebral ganglion* (Figs. 57, 79, C.) *is exposed. In adult specimens this is surrounded by part of the white body, which should be gently brushed away from the ganglion. When dissection is continued towards the sides care should be taken to leave intact the postorbital nerves* (Fig. 57, P.O.N.) *which run in a dorsal direction through the cephalic cartilage. When the superior ophthalmic nerves* (S.A.O.N. *and* S.P.O.N.), *and the optic nerves* (C.O.N.) *lying in the orbit, are exposed, remove the muscles lying posterior to the cerebral ganglion, so that the digestive glands and the oesophagus* (Fig. 57, OES.) *are uncovered. Remove the oesophagus, the cephalic artery* (Fig. 58, CE.A.), *the posterior salivary glands* (Fig. 36, P.S.G.) *and the anterior points of the digestive glands. When this has been done, the dorsal surface of the visceral ganglion* (Fig. 57, V.G.), *the visceral nerves* (V.N.), *the pallial nerves* (P.N.), *and the collar muscle nerves* (C.N.) *are exposed. Further dissection of the cartilage lateral to the visceral ganglion exposes the anterior head retractor nerves* (A.H.R.N.).

Continue the dissection on the right side only. *When the optic ganglion* (Figs. 57 *and* 67, OP.G.) *has been exposed, remove the eye, and turning the animal on to its left side, continue the dissection laterally. First remove the rest of the white body* (Fig. 67, W.B.) *which surrounds the optic ganglion, and then cut off the optic ganglion by cutting through the optic nerve just lateral to the olfactory ganglion* (Fig. 57, O.G.). *The nerves which, in addition to the superior ophthalmic nerves already mentioned, lie in the orbit, and which can be seen without further dissection, i.e., the olfactory nerve* (Figs. 28, 56, O.N.), *the anterior and posterior oculomotor nerves* (Fig. 56, A.O.M.N. *and* P.O.M.N.; Fig. 28, F.A.O. *and* P.O.M.N.), *and the inferior posterior ophthalmic nerve* (Fig. 28, F.I.P.), *should be identified, so that damage to them may be avoided in subsequent dissection. Locate the brachial nerves* (Fig. 56, B.N. 1–4) *lying just beneath the muscle forming the anterior part of the orbit, and separating the latter from the peri-buccal sinus. (These nerves actually run along the surface of the peri-buccal sinus, covered only by a membrane.) Trace them back to the brachial ganglion* (BR.G.), *and expose the superior buccal ganglion* (S.B.G.), *lying anterior to the cerebral ganglion. Expose the emergence of the anterior and posterior funnel nerves* (A.F.N. *and* P.F.N.), *and remove the rest of the cartilage which encloses the ganglia.*]

(*a*) GANGLIA.

Cerebral ganglion. (Figs. 56, 57, 79, C.; Fig. 49, unlettered).

The cerebral ganglion is a dome-shaped mass lying dorsal to the rest of the brain. Dorsally it is enclosed by the cartilage of the skull (Fig. 29, CE.C.), and in mature specimens part of the "white body" surrounds it like a padding, lying between the ganglion and the cartilage. Its originally double nature is suggested by two small grooves (Fig. 57, unlettered) along the middle line. The surface of this ganglion is marked by other grooves

(Figs. 56, 57) dividing it into several regions or lobes, to which various names have been given by different authors. The names adopted by Hillig are given here. These lobes are drawn but not lettered in Figure 56, and they should be easily recognisable from the description which follows. The most dorsal one is the vertical lobe, and immediately ventral to this on the anterior side is the superior frontal lobe. The region ventral and anterior to the superior frontal lobe is called the inferior frontal lobe, while the part of the ganglion ventral to the former and just anterior to the optic nerve (Fig. 56, C.O.N.) is called the anterior basal lobe. The corresponding region posterior to the optic nerve is called the posterior basal lobe. These two last-named lobes merge into the visceral ganglion (V.G.) and the lateral commissures (Fig. 58, C.L.C.).

Three pairs of commissures leave the cerebral ganglion. These are the lateral commissures (Fig. 58, C.L.C.) which are very stout, and almost as wide as the cerebral ganglion itself, which they unite with the visceral (V.G.) and pedal (P.) ganglia; the cerebro-buccal commissures (Figs. 56, 57, C.BU.C.); and the cerebro-brachial commissures (C.B.C.).

The following paired nerves have their origin in the cerebral ganglion (Fig. 56):

1. Optic nerves (C.O.N.).
2. Postorbital nerves (P.O.N.).
3. Superior anterior ophthalmic nerves (S.A.O.N.).
4. Superior posterior ophthalmic nerves (S.P.O.N.).
5. Olfactory nerves (O.N.).

Visceral ganglion. (Figs. 56, 57, 79, V.G.; Fig. 49, unlettered.).

If there were originally paired visceral ganglia no indication of this remains. The visceral ganglion lies with its ventral side against the statocyst cartilage (Fig. 79, SC.), and is enclosed laterally by the orbital cartilages

(Fig. 29, O.C.). Dorsally and mesially it is bounded by the peri-oesophageal blood sinus (Fig. 57, P.O.S.) and is slightly concave on this side. Viewed from the dorsal side it appears roughly rectangular in shape. Laterally it is connected to the cerebral ganglion by the lateral commissures (Fig. 58, C.L.C.). It is connected laterally also to the pedal ganglion (P.), which lies immediately anterior to it; but in the middle line (G.V.P.) the visceral and pedal ganglia are completely separated by a projection of the anterior part of the statocyst cartilage (Fig. 79, SC.), which is continued as a membrane. The paired branches of the cephalic artery (Fig. 58, CE.A.) pass here from the dorsal side of the oesophagus (OES.), through the centre of the brain between the visceral and pedal ganglia before uniting to form the anterior cephalic artery (Figs. 47, 49, A.C.A.) running immediately ventral to the pedal and brachial ganglia.

The following paired nerves have their origin in the visceral ganglion (Fig. 56):

6. Visceral nerves (V.N.).
7. Pallial nerves (P.N.).
8. Posterior head retractor nerves (P.H.R.N.).
9. Collar muscle nerves (C.N.).
10. Anterior head retractor nerves (A.H.R.N.).
11. Posterior funnel nerves (P.F.N.).

Pedal ganglion. (Figs. 56, 58, 79, P.; Fig. 49, unlettered.).

This ganglion lies between the visceral (V.G.) and brachial (BR.G.) ganglia. It is about the same size as the visceral ganglion. It is bounded ventrally partly by the statocyst cartilage, and partly by the bridge (Fig. 27, BR.) of the skull. Dorsally it is bounded by the peri-oesophageal sinus (Fig. 49, P.O.S.), and laterally it is fused with the cerebral ganglion by means of the lateral commissures (Fig. 58, C.L.C.).

The following paired nerves have their origin in the pedal ganglion (Fig. 56):

12. Anterior funnel nerves (A.F.N.).
13. Inferior posterior ophthalmic nerves (I.P.O.N.).
14. Anterior oculomotor nerves (A.O.M.N.).
15. Nerves of the cristae staticae (C.S.N.).
16. Nerves of the maculae staticae (M.S.N.).
17. Posterior oculomotor nerves (P.O.M.N.).

Brachial ganglion. (Figs. 56, 58, 79, BR.G.; Fig. 49, unlettered.)

This ganglion is smaller than the visceral and pedal ganglia. It is convex on the ventral side where it is bounded posteriorly by the anterior part of the bridge (Fig. 27, BR.; Fig. 49, unlettered) of the skull, and anteriorly by the tough membrane which covers all the ganglia. Its dorsal surface is applied to the walls of the peri-oesophageal sinus (Fig. 49, P.O.S.), so that it appears to be wrapped round the ventral wall of the latter. It is almost completely separated (Fig. 58, G.P.B.) from the pedal ganglion (P.) except laterally, by a membrane stretching from the wall of the peri-oesophageal sinus to the membrane which encloses the ganglion on the ventral side. Anteriorly the nerves to the arms and tentacles (Figs. 56, 57, B.N. 1–4 and T.N.) radiate from it. Chéron very aptly called it the goose-foot ganglion. The paired brachio-buccal commissures (Figs. 56, 57, B.B.C.) and cerebro-brachial commissures (C.B.C.) are connected to this ganglion.

The following paired nerves have their origin in the brachial ganglion (Fig. 56):

18. Brachial nerves (B.N. 1–4.).
19. Tentacle nerves (T.N.).
20. Superior antorbital nerves (S.A.N.).
21. Inferior antorbital nerves (I.A.N.).
22. Inferior anterior ophthalmic nerves (I.A.O.N.).

Superior buccal ganglion. (Figs. 37, 49, 56, 57, 79, S.B.G.).

This ganglion when compared with those previously described is quite small. It lies a short way anterior to the cerebral ganglion and is attached to the outside of the wall of the peri-œsophageal sinus (Fig. 49, P.O.S.). It is somewhat dorso-laterally compressed, oval in surface view, and shows a very slight longitudinal groove on its ventral surface, which probably indicates the double origin of this ganglion.

The following commissures link it up with the other parts of the nervous system: the cerebro-buccal commissures (Figs. 56, 57, C.BU.C.), the brachio-buccal commissures (B.B.C.), and the superior inferior buccal commissures (Figs. 37 and 49, C.B.S.), which connect the superior and inferior buccal ganglia. (The latter [Fig. 49, I.B.G.] is included in the description of the sympathetic system.)

A large number of nerves have their origin round the margin of the superior buccal ganglion.

These are:

23. Labial nerves.

(*b*) COMMISSURES.

Although the commissures have already been referred to in the description of the ganglia, for convenience they are described below under individual headings.

Lateral commissures. (Fig. 58, C.L.C.)

These are very stout commissures uniting the cerebral ganglia with the visceral and pedal ganglia, in this way completing the ring of nervous tissue which surrounds the oesophagus.

Cerebro-buccal commissures. (Figs. 56, 57, C.BU.C.)

These run from the inferior frontal lobe of the cerebral

ganglion to the posterior side of the superior buccal ganglion. They are quite slender, and run almost along the middle line, attached to the membrane bounding the peri-oesophageal sinus.

Cerebro-brachial commissures. (Figs. 56, 57, C.B.C.)

These are slender commissures linking the cerebral and brachial ganglia. They run in the membrane dividing the peri-oesophageal sinus from the peri-buccal sinus, at the posterior limit of the latter, and along the posterior margins of the paired foramina (Fig. 49, F.O.B.) which occur in this membrane.

Brachio-buccal commissures. (Figs. 56, 57, B.B.C.).

These connect the superior buccal ganglion (Fig. 56, S.B.G.) and the brachial ganglion (BR.G.). They are quite slender and run first dorsally from the brachial ganglion close to the cerebro-brachial commissures, and just anterior to them; then they curve round anteriorly and run just lateral to the cerebro-buccal commissures to enter the posterior side of the superior buccal ganglion.

Superior inferior buccal commissures. (Figs. 37, 49, C.B.S.).

These pass on either side of the oesophagus, connecting the superior buccal and the inferior buccal ganglia (Fig. 49, S.B.G. and I.B.G.). They leave the sides of the superior buccal ganglion and run first anteriorly and then ventrally, to the sides of inferior buccal ganglion, which is attached to the postero-ventral surface of the buccal mass, just where the oesophagus emerges from the latter. For part of their course, these commissures lie freely in the peri-oesophageal sinus (P.O.S.).

B. Peripheral Nervous System.

[DISSECTION.—Continued from page 104.—*Slit open the mantle cavity by means of a longitudinal incision. The*

visceral nerves (Fig. 6, V.N.) *can be picked up running beside the cephalic vein just anterior to the anus. These can be followed to the branchial ganglia* (Figs. 54, 55, B.GA.) *without dissection. Follow the numerous branches of the visceral nerves* (Fig. 55.). *The stellate ganglia are located on the wall of the mantle cavity* (Fig. 5, S.G.). *The fin nerves* (Figs. 31, 55, F.N.) *are best followed from the dorsal side. They lie just ventral to the dorsal fin muscles* (Figs. 31, 32, D.F.M.). *The rest of the nerves should be followed from the brain to their destinations.*]

(*a*) NERVES OF CEREBRAL GANGLION.

1. Optic nerves. (Figs. 56, 57, C.O.N.).

The optic nerves which are very stout, are given off from the sides of the cerebral ganglion. They do not run quite laterally, but slightly forwards and upwards. A short way after leaving the brain each optic nerve has a little ganglion (Figs. 56, 57, O.G.) the olfactory or pedunculate ganglion attached to its dorsal surface. The latter name is probably the more suitable, as according to Jatta (1887) this ganglion has no connection with the olfactory nerve, and Klemensiewicz (1878) claims that in *Eledone* it is the seat of control of the chromatophores. Each of these ganglia is about the size of a pin's head. After travelling a short distance from the brain the optic nerve swells out into a large kidney-shaped optic ganglion (Fig. 57, OP.G., Fig. 58, C.O.G.). The longitudinal axis of this ganglion is at about 20 degrees to the main axis of the animal. Its convex side faces slightly downwards and towards the exterior, while the hilus, or depressed part, lies dorsally and mesially.

The retinal nerves (Figs. 57, 67, RE.N.) are given off from all over the surface of the ganglion, in the form of loose bundles. The mass of retinal nerves is flattened dorso-laterally. The dorsal and ventral nerves from the middle region of the ganglion are interlaced, so that the

nerves from the ventral side enter the eyeball more dorsally than those from the dorsal side. The bundles of retinal nerves enter the eyeball separately (Fig. 60, F.R.N.) over a large area.

2. Postorbital nerves. (Figs. 56, 57, P.O.N.).

Each postorbital nerve has its origin at the posterior edge of the optic nerve. It is a fairly stout nerve, which runs almost vertically through the skull. Immediately after leaving the skull it divides into numerous branches which pass into the anterior part of the retractor muscles of the head.

3. Superior anterior ophthalmic nerves. (Figs. 28, 56, 57, S.A.O.N.).

The superior anterior ophthalmic nerve arises just lateral to the postorbital nerve. It passes into the orbit through the foramen of the optic nerve, and is dorso-ventrally flattened. Soon after leaving the cerebral ganglion it forks into two main branches, which lie on either side of the ophthalmic artery (Fig. 28, O.A.). This nerve innervates the superior oculomotor muscles, I, II, and III (Fig. 61, M.SU., I-III.). In addition, it sends fine branches to the skin dorsal to the eye, the surface of the eyeball, and the iris.

4. Superior posterior ophthalmic nerves. (Figs. 56, 57, S.P.O.N.).

This nerve has its origin just posterior to the superior anterior ophthalmic nerve. It is dorso-ventrally flattened, and after passing through the skull (Fig. 28, F.S.P.), it forks into two branches. It innervates the posterior oculomotor muscles I and II (Fig. 61, M.P., I and II).

5. Olfactory nerves. (Figs. 29, 56, O.N.).

The olfactory nerve arises on the postero-ventral edge of the optic nerve. It enters the orbit through the foramen of the optic nerve, and runs along the surface of the orbital cartilage (Figs. 27, 28, 29, O.N.), and passes

through the wing of the orbital cartilage (Fig. 27, W.O.), to the olfactory pit (Fig. 1, O.P.), which lies in the skin just posterior to the eye.

(*b*) NERVES OF VISCERAL GANGLION.

6. Visceral nerves. (Figs. 5, 23, 24, 25, 49, 55, 56, 57, V.N.).

These nerves have their origin on the posterior surface of the visceral ganglion (Fig. 57, V.N.) close together near the middle line. They pass through the foramen magnum (Fig. 26, E.V.N.) close to the ventral rim of the latter, and run together obliquely and posteriorly between the two digestive glands (Fig. 49, V.N.). As they approach the ventral surface of the capsule enclosing the digestive glands (L.), the two nerves separate slightly. They pass through paired foramina (Figs. 23, 33, unlettered) in the diaphragm cartilage (D.CA.) and then run posteriorly immediately lateral to the cephalic vein (Fig. 5, CE.V.), and just under the membrane which attaches the latter to the visceral dome. Just before they pass through the diaphragm cartilage each gives off a small branch (Fig. 55, P.C.N.), the posterior nerve of the cephalic vein, which passes, with the main nerve, through the diaphragm cartilage, and innervates the wall of the muscular chamber (Fig. 23, M.CE.V.) of the cephalic vein, sending branches both anteriorly and posteriorly.

Just after passing through the diaphragm cartilage the visceral nerve gives off a large branch (Figs. 6, 23, 55, N.R.F.) which runs laterally and slightly posteriorly over the ventral surface of the capsule of the digestive glands to the retractor muscle of the funnel, which it innervates. This nerve, which can be seen without dissection (Fig. 6, N.R.F.) when the mantle cavity and funnel are slit open, is called the nerve of the retractor muscle of the funnel.

The main visceral nerve continues posteriorly beside the cephalic vein. A short way anterior to the anus, it gives off a branch, the inksac nerve (Fig. 55, IS.N.) which runs posteriorly, at first in the muscular membrane (Fig. 23, A.RE.) attaching the rectum to the sheath of the digestive gland. On reaching the rectum and ink duct it splits up, sending branches to the anterior and posterior regions of the inksac and to the rectum. One or two of the branches of the left and right inksac nerves to the anterior part of the inksac unite, forming a small commissure, the anterior visceral commissure (Fig. 55, A.V.C.).

At the point where the cephalic vein (Fig. 20, CE.V.) forks into venæ cavæ (V.C.), the visceral nerves (V.N.) also fork. Each divides into an outer and an inner branch. The outer branch which is called the branchial nerve (Fig. 55, BR.N., Fig. 54, unlettered) runs postero-laterally in the anterior wall of the renal sac to the base of the branchia, where it swells into the branchial ganglion (Figs. 54, 55, B.GA.), and then passes into the branchia itself, running through the centre of the latter, just ventral to the axial part (Fig. 54, A.R.B.) of the retractor muscle of the branchia. The inner branches of the two visceral nerves fuse up ventral to the cephalic vein, to form the comparatively large posterior visceral commissure (Fig. 55, P.V.C.). Several pairs of nerves leave this commissure, innervating the renal papillæ and walls of the renal sac (R.N.), the nidamental glands (N.G.N.) in the female, and the systemic heart (CA.N.).

The left branchial nerve, just after leaving the main visceral nerve, gives off a branch (G.D.N.), which innervates the whole of the genital duct, both in the male and female. The branchial ganglion (Figs. 54, 55, B.GA.) is rounded and oval in form. It sends out numerous fine branches, to the auricle, the retractor muscles of the branchia, and to the branchial heart.

7. Pallial nerves. (Figs. 24, 25, 55, 56, 57, P.N.).

Each of the pallial nerves which, next to the optic nerves are the largest in the body, emerges from the lateral part of the posterior side of the visceral ganglion (Fig. 57, P.N.). It passes through the foramen magnum (Fig. 26, E.P.N.) a little lateral to the visceral nerve, and runs postero-laterally between the dorsal and ventral anterior lobes of the digestive gland (Fig. 36, P.N.). It passes through the retractor muscle (Fig. 25, R.H.) of the head, and immediately divides into two equal branches. The outer one after a short distance enters the stellate ganglion (Figs. 25, 55, S.G.), which can be seen (Fig. 5, S.G.) without dissection when the mantle is opened. The stellate ganglion is a large roughly triangular mass of nervous tissue, from the outer margin of which numerous nerves radiate, which, after running a short distance just beneath the skin which lines the mantle cavity, penetrates the muscular wall of the latter. A few nerves also leave the dorsal surface of this ganglion. According to Bozler (1927) the stellate ganglion is a motor centre for the mantle, and Cate (1929a) claims to have produced reflex action through it.

The inner branch of the pallial nerve runs mesial to the stellate ganglion. It is joined to the latter by two commissures (Fig. 55, unlettered), which enter it on the dorsal side, and then it passes through the mantle wall, and divides into numerous very large flattened branches, the nerves of the fin (Figs. 31, 55, F.N.), which spread out in fan-like fashion, and enter the fin at intervals throughout its length from the dorsal side, passing first lateral to and then through the fin cartilage. Numerous nerves (Figs. 32, 55, D.S.N.) leave the main fin nerve and innervate the skin of the back, and the shell sac.

8. Posterior head retractor nerves. (Figs. 55, 56, 57, P.H.R.N.).

This nerve, which compared with the pallial nerve is quite

slender, emerges from the brain close beside the latter, on the mesial side. It runs with the corresponding pallial nerve until both reach the retractor muscle (Fig. 25, R.H.) of the head. Here while the pallial nerve passes through, the posterior retractor muscle nerve enters the muscle, the posterior part of which it innervates.

9. Collar muscle nerves. (Figs. 55, 56, 57, C.N.).

This nerve emerges from the visceral ganglion close to the corresponding pallial nerve, but a little anterior and dorso-lateral to it. It runs postero-laterally, passing through the skull cartilage (Fig. 26, F.C.N.) dorso-laterally to, but very close to the emergence of the pallial nerve. After leaving the skull it runs, at first, in loose connective tissue, so that it can easily be seen in a dorsal dissection of the central nervous system. After travelling a short distance immediately posterior to the large posterior funnel artery (Fig. 49, P.FU.A.), it enters the collar muscles of the funnel (Fig. 25, I.C.F. and O.C.F.), which it innervates.

10. Anterior head retractor nerves. (Figs. 55, 56, 57, A.H.R.N.).

This nerve emerges from the visceral ganglion anteriorly and dorso-laterally. It is laterally compressed, and travels postero-laterally for some distance through the skull, giving off one or two very fine branches. The main nerve emerges through its own foramen (Fig. 26, F.A.H.) which lies a little lateral to the foramen of the collar muscle nerve, and innervates the anterior part of the retractor muscle of the head.

11. Posterior funnel nerves. (Figs. 23, 56, P.F.N.).

This nerve has its origin on the ventral surface of the visceral ganglion. It runs through the skull cartilage postero-ventrally and lateral to the statocyst. After leaving the skull (Figs. 26, 27, F.P.F.) it runs posteriorly

for a short distance inside the capsule of the digestive gland, so that it can be easily seen in the dissection of the central nervous system from the dorsal side, when the digestive glands are removed. Then it passes through the muscular sheath of the digestive glands, and curves round to run postero-laterally (Fig. 23, P.F.N.) close beside the posterior funnel artery (Fig. 47, P.FU.A.) to the lateral part of the funnel which it innervates. Shortly after leaving the skull this nerve gives off a slender branch which travels with it for some way, and then innervates the anterior part of the muscular chamber (Fig. 23, M.CE.V.) of the cephalic vein. This is the anterior nerve of the cephalic vein. Hillig describes the latter nerve as having an independent origin in the visceral ganglion, just posterior to the origin of the posterior funnel nerve. Probably this origin is a little variable.

(*c*) NERVES OF PEDAL GANGLION.

12. Anterior funnel nerves. (Figs. 23, 49, 56, A.F.N.).
13. Inferior posterior ophthalmic nerves. (Figs. 55, 56, I.P.O.N.).

The anterior funnel nerve has its origin on the posterior ventral side of the pedal ganglion. It is a thick nerve, which passes ventrally through the skull (Figs. 25, 27, F.A.F.). Soon after emerging from the skull it divides into five branches. The outermost and smallest of these branches (Fig. 56, I.P.O.N.) passes through the orbital cartilage (Fig. 28, F.I.P.) and travels over the surface of the cartilaginous part of the orbit and along the anterior edge of the wing (Fig. 29, W.O.) of the orbital cartilage. This is the inferior posterior ophthalmic nerve (Fig. 56, I.P.O.N.) which innervates the posterior part of the eyelid. The other four branches of the anterior funnel nerve

spread out somewhat (Fig. 23, A.F.N.) and enter the dorsal wall of the funnel.

14. Anterior oculomotor nerves. (Fig. 56, A.O.M.N.).

This nerve has its origin on the anterior side of the pedal ganglion (P.) where it emerges into the brachial ganglion (BR.G.). It is quite a broad nerve, which passes through the skull (Fig. 28, F.A.O.) and enters the orbit. After a short distance it breaks up into numerous branches innervating the trochlear oculomotor muscles I, II, and III. (Fig. 64, M.TR., I and II ; Fig. 65, M.TR., III.), the inferior oculomotor muscle II (Fig. 63, M.I., II.), the anterior oculomotor muscle I (Fig. 65, M.A., I.) and the conjunctive muscle I (Fig. 64, M.A.C., I.). The branch to trochlear muscle III is especially conspicuous. It runs outwards under trochlear muscle II, to the middle of trochlear muscle III, which it enters.

15. Nerves of cristae staticae. (Fig. 56, C.S.N.).

This nerve emerges from the ventral side of the posterior part of the pedal ganglion. It runs postero-laterally in the statocyst cartilage, forking into two branches which innervate the crista statica (Fig. 68, C.ST.) of the statocyst.

16. Nerves of maculae staticae. (Fig. 56, M.S.N.).

This nerve has its origin just medial to the nerve of the crista statica. It runs slightly more ventrally and mesially, passing through the anterior wall of the statocyst cartilage to the macula (Fig. 68, M.ST.) of the statocyst. Before it reaches the macula it divides into two branches.

17. Posterior oculomotor nerves. (Figs. 28, 56, P.O.M.N.).

This nerve has its origin on the side of the pedal ganglion (Fig. 56, P.) near the postero-ventral edge of the optic nerve (C.O.N.). It passes together with the olfactory

nerve (O.N.) through the foramen of the optic nerve, and runs over the postero-ventral surface of the orbit, lying against the orbital cartilage. It innervates the inferior oculomotor muscle I (Fig. 63, M.I., I.).

(*d*) NERVES OF BRACHIAL GANGLION.

18. Brachial nerves. (Figs. 56, 57, B.N., 1-4; Fig. 55, B.N.).

The four pairs of brachial nerves which innervate the arms are given off from the anterior end of the brachial ganglion (Fig. 58, BR.G.). They are somewhat flattened, and run at first along the inner surface of the peri-buccal blood sinus, in which lies the buccal mass. When the peri-buccal sinus is opened the brachial nerves can be seen, lying beneath the membrane which lines the wall of the sinus. Half way towards the anterior end of the peri-buccal sinus, the brachial nerves enter the muscular bases of the arms. A little further on their course each of them swells up into a small ganglion (Fig. 56, unlettered). All the eight ganglia are joined by the interbrachial commissure (Fig. 56, IB.C.) which forms a complete ring. Numerous small nerves are given off from these ganglia, which enter the muscles of the bases of the arms. In addition each of these ganglia gives off a nerve (Figs. 55, 56, B.P.N.) to the corresponding buccal pillar, as the pieces of radial webbing which support the buccal funnel (Fig. 7, B.F.) have been called. The buccal pillars at the bases of the dorsal pair of arms have become fused. This is confirmed by the fact that this pillar is innervated by two nerves. Beyond the interbrachial commissure each of the brachial nerves, accompanied by the brachial artery, enters the corresponding arm, up the centre of which it runs (Fig. 50, B.N.), giving off numerous branches to the suckers.

19. Tentacle nerves. (Figs. 55, 56, 57, T.N.).

The tentacle nerves are given off from the anterior end of the brachial ganglion (Fig. 58, BR.G.) between the nerves to arms 3 and 4. Each enters the base of the corresponding tentacle, up the centre (Fig. 51, T.N.) of which it runs, accompanied by the tentacle artery, to the tip, where it gives off numerous branches to the suckers of the tentacle. The tentacle nerves pass outside the interbrachial commissure.

20. Superior antorbital nerves. (Fig, 56, S.A.N.).

These nerves which are several in number, and a little variable, emerge from the anterior dorsal side of the brachial ganglion and from the dorsal pair of brachial nerves. They innervate the dorsal muscles of the head.

21. Inferior antorbital nerves. (Fig. 56, I.A.N.).

These consist of four small nerves on each side, which emerge from the ventral side of the brachial ganglion close to the origin of the tentacle nerves and the fourth brachial nerves. They innervate the ventral muscles of the head.

22. Inferior anterior ophthalmic nerves. (Fig. 56, I.A.O.N.).

This is quite a large nerve which emerges from the brachial ganglion close to the tentacle nerve. It runs in the muscle of the ventral anterior wall of the orbit, to the anterior part of the muscular eyelid (Fig. 59, EL.), which it innervates. If the tentacle pocket is opened, this nerve can be seen without further dissection, running outwards in the dorsal wall of the latter, just under the skin which lines it.

(*e*) Nerves of Superior Buccal Ganglion. (Figs. 37, 56, S.B.G.).

23. Labial nerves.

In addition to the commissures, a large number of labial

nerves radiate from the superior buccal ganglion. These first run in a delicate membrane which lies immediately within the retractor muscles of the buccal mass, and to which the latter are applied. Then they pass over the whole surface of the buccal mass, and innervate the lips.

C. Sympathetic Nervous System.

(*a*) INFERIOR BUCCAL GANGLION. (Figs. 36, 49, I.B.G.).

This ganglion is situated on the postero-ventral side of the buccal mass, where the œsophagus emerges from it. It lies directly ventral to the superior buccal ganglion (Figs. 37, 49, S.B.G.) with which it is connected by the superior inferior buccal commissure (Figs. 37, 49, C.B.S.). This ganglion is rectangular in surface view, dorso-ventrally flattened, and its long axis is transverse. Numerous nerves leave it.

(*b*) NERVES OF INFERIOR BUCCAL GANGLION.

1. Mandibular nerves.

These emerge from the anterior corners of the ganglion and run forwards along the ventral side of the buccal mass, which they innervate.

2. Maxillary nerves.

These arise at the sides of the ganglion, and innervate the dorsal jaw muscles. In addition numerous very fine nerves leave this ganglion and enter the buccal mass.

3. Sympathetic nerves. (Figs. 36, 55, S.N.).

The two sympathetic nerves emerge from the posterior side of the inferior buccal ganglion (Fig. 36, I.B.G.) near the middle line. They run along the sides of the oesophagus (OES.) to the stomach (ST.) as thin nerves, passing with the former through the centre of the brain.

(*c*) GASTRIC GANGLION. (Figs. 36, 55, G.G.).

On the anterior ventral side of the stomach, close to the beginning of the intestine, the sympathetic nerves

enter the large gastric ganglion, which is elongated and oval in surface view, and flattened against the wall of the stomach, to which it is attached.

(*d*) NERVES OF GASTRIC GANGLION.

A large number of nerves leave the gastric ganglion, the chief of which are :—

1. Nerves of ducts of digestive glands. (Fig. 55, L.D.N.).
2. Nerves of stomach. (Fig. 55, ST.N.).
3. Nerves of caecum. (Fig. 55, CAE.N.).
4. Nerve of intestine, which runs along the dorsal side of the intestine.

SENSE ORGANS.

A. Eye.

Unlike the tetrabranchiate eye, as represented by *Nautilus*, the dibranchiate eye is very highly developed, and will compare quite favourably with the eyes of many Vertebrates.

The cephalopod and vertebrate eyes show a very remarkable degree of parallel evolution. Although close analogies can be drawn between the corresponding parts, homologically they are fundamentally different. For while the vertebrate eye is formed by an outgrowth of the brain, the cephalopod eye is formed by an invagination of the ectoderm. In the cephalopod eye the optic nerves enter the retina from behind, in separate bundles, instead of in front from a single nerve, and there is no choroid, and a non-cellular lens. There is also no anterior aqueous chamber, and the so-called cornea is a continuation of the orbital wall and not connected with the eyeball. Only rods occur in the retina, and in this respect the cephalopod eye agrees with that of some nocturnal birds.

Many important works have appeared, dealing with various aspects of the cephalopod eye. Grenacher's work (1886) on the retina was the first which clearly illustrated its structure, and the work of Hesse (1900) on the same subject includes some fine figures.

More recent writers have concerned themselves chiefly with the accommodation of the eye, and with the mechanism of sight. Very conflicting opinions on these subjects have been voiced, among which should be mentioned those of Beer (1897), Hesse (1900), Hess (1905 and 1909), Heine (1907), and Alexandrowicz (1927). The last-mentioned author gives an excellent account, including histological detail, of the structure of the eye.

Several of the earlier authors were aware of the existence of extrinsic eye muscles. Krohn (1835) gave a fair description of them, but without figures. Owen (1836) described four in *Sepia*. Hensen (1865) published a general description of them. An admirable comparative account, well illustrated, of cephalopod eye muscles was given by Glockauer (1915). *Sepia officinalis* was one of the nine decapod types studied, and Glockauer calls special attention to the pecularities in the eye musculature of *Sepia*.

The eyes (Fig. 1, unlettered) bulge a little from the dorso-lateral sides of the head. Each lies within a large orbit (Fig. 59, OR.), composed anteriorly of a muscular wall, and posteriorly of the orbital cartilage of the skull (Fig. 61, O.C.). They point slightly forwards and upwards.

The wall of the eyeball consists of three layers. On the outside is the metallic-coloured argentea, which is a membrane continuous with that which lines the orbit. Next to this lies the sclera (Figs. 60, 66, 67, SC.CA. and E.C.), which is composed partly of thin cartilage and partly of fibrous tissue. It is not rigid enough to preserve the form of the eye when the latter is removed from the animal. The inside of the eyeball is filled with liquid aqueous

humour and lined by the retina (Fig. 67, O.F.R. and P.L.R.). The retinal nerves enter the mesial surface of the eyeball in individual bundles (Fig. 60, F.R.N., Fig. 67, RE.N.) over a large area.

A large almost spherical lens (Fig. 67, LE.) is held in place by a ciliary body (Figs. 66, 67, CI.M. and E.B.). On the outside the lens is surrounded by a highly contractile iris (Figs. 59, 66, 67, IR.).

The eyeball is held in place by a membrane called the external argentea (Figs. 59, 66, E.A.), which completely surrounds it, stretching from the pupil to the insertion of the eye on to the orbital cartilage. Immediately beneath this membrane, and running from their origin on various regions of the cartilaginous part of the skull to their insertion, mostly in the equatorial region of the eyeball, are numerous rather delicate eye muscles (Figs. 61 to 65). The trochlear cartilage (Figs. 27, 29, 63, 64, 66, TR.) of the skull is covered by the external argentea, and in this way bound to the anterior surface of the eyeball. Several eye muscles run from it to their insertion on the surface of the eyeball. Many of the oculomotor muscles are closely attached to the external argentea.

The eyeball contains no true cornea. The so-called cornea consists of a horny membrane (Fig. 59, COR.), which completes the orbit laterally. In life the cornea is perfectly transparent, and is distended by the fluid which fills the orbit, so that it bulges convexly from the surface of the head. It forms a sort of window in the orbit for the eye to see through, but apparently plays little or no part in focussing. Curving round the cornea on the ventral side is a large muscular eyelid (EL.), which can be completely drawn over the cornea by the contraction of its longitudinally placed muscles. Retraction of the eyelid appears to be achieved by the contraction of the skin. The orbit communicates with the exterior by means of a

tiny pore, located under the anterior end of the eyelid. This leads to the orbit *via* a short duct (Figs. 59, 67, D.O.).

(*a*) OCULOMOTOR MUSCLES.

The nomenclature of the oculomotor muscles has been adopted from Glockauer. They are called, superior, inferior, anterior or posterior, according to the part of the orbit on which they have their origin. In addition there are three trochlear muscles, whose origin is on the trochlear cartilage, and two conjunctive muscles whose tendons are continuous with those of the opposite eye. Where two or three muscles arise on the same side of the eye, they have been numbered I, II, and III, number I always lying on the outside, and number III within or partly within number II. Altogether 13 eye muscles can be recognised. Although some of them are comparatively stout, others are extremely thin, and their dissection is a delicate operation, requiring suitably preserved material. Most of the muscles are, however, quite distinct, and very constant in different specimens.

[DISSECTION :—*It is best to use large specimens, which have not been unduly hardened in formalin, and which have been subsequently soaked in water for some weeks. This usually makes the muscles show up better. Isolate the skull, leaving the eyes attached to the cartilage of the orbits. Take great care not to damage the external argentea which attaches the eyes to the orbital cartilages. Using a hypodermic syringe, inject water into the eyeball. When this is done the whole eye should become turgid. In a well-preserved specimen most of the eye muscles can now be seen without dissection, showing through the external argentea. This membrane should be stripped off from the muscles lying immediately beneath it. This requires care as some of the more delicate muscles are liable to come away with it. When the external argentea has been removed, the individual muscles, some of which lie partly on top of others, can be separated.*]

MUSCLES OF DORSAL SIDE.

1. Superior muscle I. (Fig. 61, M.SU., I.).

The origin of this muscle is on the dorsal and postero-dorsal edge of the orbital cartilage. It is very broad and runs postero-laterally in an oblique course, passing under posterior muscle II (M.P., II). Its insertion on the equator of the eye is very delicate. The anterior margin of this muscle is quite distinct, but the posterior edge is blended with the other muscles. This muscle is innervated by the superior anterior ophthalmic nerve (Figs. 29, 56, S.A.O.N.).

2. Superior muscle II. (Fig. 61, M.SU., II).

The origin of this muscle is the dorsal edge of the orbital cartilage immediately under superior muscle I (M.SU., I). It is a little thicker than the latter and runs laterally with fan-like expansion to its insertion on the dorsal side of the equator of the eye. This muscle is innervated by the superior anterior ophthalmic nerve (Figs. 29, 56, S.A.O.N.).

3. Superior muscle III. (Fig. 61, M.SU., III).

This muscle lies under both the other superior eye muscles. It is slender but easily the most powerful of the three. Its origin is on the dorsal edge of the orbital cartilage, and it runs anteriorly and laterally in an oblique course to the antero-dorsal region of the equator of the eye where it is inserted. At its insertion it spreads out somewhat. This muscle is innervated by the superior anterior ophthalmic nerve (Figs. 29, 56, S.A.O.N.).

MUSCLES OF POSTERIOR SIDE.

4. Posterior muscle I. (Figs. 61, 62, M.P., I.).

This is a very delicate and slender muscle. Its origin is on the posterior border of the orbital cartilage and it runs obliquely dorsally to its insertion on the equatorial cartilage in the neighbourhood of the iris artery (Fig. 61,

IR.A.). This is the most delicate of all the eye muscles of *Sepia*. It is innervated by the superior posterior ophthalmic nerve (Figs. 29, 56, S.P.O.N.).

5. Posterior muscle II. (Fig. 62, M.P., II.).

This is an extremely broad muscle. Its origin is on a large part of the posterior and postero-dorsal edge of the orbital cartilage. It has a delicate structure, and travels laterally with a slight increase of breadth to its insertion on the equatorial cartilage, passing outside part of superior muscle, I (M.SU., I). This muscle is innervated by the superior posterior ophthalmic nerve (Figs. 29, 56, S.P.O.N.).

MUSCLES OF VENTRAL SIDE.

6. Inferior muscle I. (Fig. 63, M.I., I).

This is the most powerful of all the eye muscles. Its origin is on the postero-ventral edge of the orbital cartilage within the wing of the orbital cartilage. It runs anteriorly and obliquely, first decreasing in breadth, and then broadening out, to its insertion on the equatorial cartilage. Its importance is emphasised by the fact that the distribution of the posterior oculomotor nerve (Figs. 29, 56, P.O.M.N.) which innervates it is limited to this muscle alone.

7. Inferior muscle II. (Fig. 63, M.I., II).

This muscle has a very slender tendon-like origin at the angle formed by the trochlear (TR.) and orbital (O.C.) cartilages. It runs outwards and slightly posteriorly, with fan-like expansion to its insertion on the equatorial cartilage. It is innervated by the anterior oculomotor nerve (Fig. 28, F.A.O.; Fig. 56, A.O.M.N.).

MUSCLES OF MEDIAN ANTERIOR SIDE.

The two conjunctive muscles are so-called because their tendons are connected with those of the other side.

8. Anterior conjunctive muscle, I. (Fig. 64, M.A.C., I).

This muscle runs out from the dorsal side of the bridge of the orbital cartilage (Fig. 27, BR.), as a slender but very strong tendon. It travels slightly to the dorsal side of the trochlear cartilage (Fig. 64, TR.), and broadens out somewhat before its insertion on the anterior surface of the eyeball, somewhat mesial to the equatorial cartilage. This muscle is innervated by the anterior oculomotor nerve (Fig. 28, F.A.O. ; Fig. 56, A.O.M.N.).

9. Anterior conjunctive muscle, II. (Fig. 64, M.A.C., II).

This is vestigial in *Sepia*, though very easily recognisable. It consists of a tough little tendon passing from the other eye across the anterior surface of the bridge of the orbital cartilage (Fig. 27, BR.), and over the ventral surface of the base of the trochlear cartilage (Fig. 64, TR.). Glockauer states that the reduction of the conjunctive muscles goes hand in hand with the broadening of the trochlear cartilage. He claims that this is an advance in body organisation, and on this ground says that *Sepia* is more highly developed than *Loligo* or *Rossia*.

10. Trochlear muscle I. (Fig. 64, M.TR., I).

This is a delicate muscle which arises from the posterior surface of the trochlear cartilage (TR.), and runs out dorso-laterally with fan-like expansion to its insertion on the anterior surface of the eye. It is inserted under anterior conjunctive muscle I (M.A.C., I). This muscle is innervated by the anterior oculomotor nerve (Fig. 28, F.A.O. ; Fig. 56, A.O.M.N.).

11. Trochlear muscle II. (Fig. 64, M.TR., II).

This is a strong muscle. Its origin is on the ventral side of the trochlear cartilage (TR.) and it runs laterally, with fan-like expansion to its insertion on the equatorial cartilage. Its distal end is very delicate. Part of the

origin of this muscle is fused with that of anterior muscle I (Fig. 65, M.A., I). It is innervated by the anterior oculomotor nerve (Fig. 28, F.A.O. ; Fig. 56, A.O.M.N.).

12. Trochlear muscle III. (Figs. 60, 65, 66, M.TR., III) .

This is a slender but strong muscle which arises from the posterior surface of the trochlear cartilage (Fig. 66, TR.) near the apex. It runs posteriorly and ventrally to its insertion on the mesial surface of the eyeball, ventral to the entry of the retinal nerves. This muscle is innervated by the anterior oculomotor nerve (Fig. 28, F.A.O. ; Fig. 56, A.O.M.N.).

13. Anterior muscle I. (Fig. 65, M.A., I).

The origin of this muscle lies just under the base of the trochlear cartilage. It is a strong muscle which runs out laterally, beneath the trochlear cartilage, to its insertion on the anterior part of the eyeball. Its origin is somewhat fused with that of trochlear muscle II (Fig. 64, M.TR., II), so that it is difficult to say whether part of the latter should be included in the former. Glockauer, from his figure and description of this muscle in *Sepia*, evidently does include what seems to be part of trochlear muscle II, as part of anterior muscle I. It is innervated by the anterior oculomotor nerve (Fig. 28, F.A.O. ; Fig. 56, A.O.M.N.).

Conflicting views have been put forward as to the extent to which the Cephalopods can move their eyes. Henson (1865) considered that the proximity of the optic ganglion to the eyeball makes extensive eye movements unthinkable, and also that the sclera is not rigid enough to permit of movements of the whole eyeball. Beer (1897), however, found that the optic ganglion does not obstruct movements of the whole eye, and came to the conclusion that Cephalopods can move their eyes in all directions, but that the extent of this faculty varies immensely in different forms. Magnus (1902) confirmed the movement

in all directions of the eye of Octopods, and Muskens (1904) claimed that he produced by electrical stimulation of the eye of Octopods a compensatory rotation of 90 degrees. One has only to watch *Sepia* living in an aquarium to see that it does move its eyes, though the extent of the movement does not appear to be as great as in many fishes.

From the comparative work of Glockauer, it appears that the eye muscles of Decapods are fairly constant. This is rather remarkable, when one considers how numerous and how delicate these muscles are. Evidently the reason for having so many delicate muscles is that the eyeball is not rigid enough to withstand the effects of a few powerful muscles.

It is difficult to say in *Sepia* what effect the individual muscles have. Indeed, the posterior muscle I, which, in the Decapods generally is very weakly developed, can have little effect at all. But there can be no doubt that a limited degree of movement in all directions is possible on anatomical grounds, and probably several muscles contribute to each individual movement.

(*b*) HORSESHOE CARTILAGE. (Figs. 60, 67, H.C.).

This is a delicate piece of cartilage which curves round the dorsal and posterior mesial surface of the eyeball, lying close against the sclera. The surface which lies against the latter is slightly curved, and in transverse section (Fig. 67, H.C.) it has the form of a flat triangle, the apex of which is formed by a slight ridge on the mesial side of the cartilage. It is loosely attached to the eyeball and the orbital cartilage by muscle fibres. Its function appears to be to reinforce the sclera.

(*c*) SCLERA.

The sclera consists of two fairly distinct regions, the sclerotic cartilage (Figs. 60, 66, 67, SC.CA.) and the equatorial cartilage (E.C.), bound together by connective

tissue. The sclerotic cartilage forms the mesial part of the eyeball. It is partly cartilaginous and partly fibrous, and varies very considerably in thickness in different regions, being thickest on that part which lies ventral to the zone in which the retinal nerves (Fig. 60, F.R.N.) pass through it. These variations doubtless play a part in the functioning of the eye but their significance is difficult to determine. Where the retinal nerves pass through it this cartilage is pierced by numerous little holes (about 300 according to Alexandrowicz).

The equatorial cartilage is a ring of cartilage lying immediately next to the sclerotic cartilage in the equator region of the eyeball. It serves for the attachment of most of the oculomotor muscles, though a few of the latter are attached to the sclerotic cartilage. A thin but tough transparent membrane (Fig. 66, S.P.I.) continuous with the equatorial cartilage, forms a centrally situated support for the iris.

(*d*) IRIS. (Figs. 59, 66, 67, IR.).

The iris is built up of three layers, consisting of the external layer continuous with the argentea, which covers the whole eyeball, the sclerotic plate (Fig. 66, S.P.I.), and an internal or pigmented layer. It surrounds a crescent-shaped pupil, formed by a very prominent dorsal flap of the iris jutting into what would otherwise have been a circular diaphragm. The iris is highly muscular and the pupil can be enlarged or decreased within wide limits.

(*e*) CILIARY BODY. (Figs. 66, 67).

This term has been used by Alexandrowicz to include two structures, the circular ciliary muscle (CI.M.), which plays an important part in accommodation, and the epithelial body (E.B.) which both secretes and supports the lens.

(*f*) LENS. (Figs. 66, 67, LE.).

This is very large, roughly spherical, and lies a little anterior to the middle of the eyeball. It has a non-cellular structure, and is secreted by the epithelial body (E.B.) as two closely applied convex lenses, separated by that body. The lens which lies within the eyeball is larger than the outer one, and the two lenses together form a sphere. This spherical lens is of fixed focal length.

(*g*) RETINA. (Figs. 66, 67, O.F.R. and P.L.R., Fig. 71).

The retina appears as a tissue which separates very readily from the sclera, except in the region of the ciliary body where the retinal nerves (Fig. 67, RE.N.) pass through the sclerotic cartilage. It is fairly thick but becomes rapidly thinner at the level of the equatorial ring. Here it loses its visual elements, and lines the ciliary body as only a pigmented epithelium. In preserved specimens the retina usually separates into three layers, composed of the very thin limiting membrane (Fig. 71, L.M.) internally, the rod layer (R.), in which the pigment has become concentrated on the outer surface which is coloured a very dark brown in consequence, and externally the optic fibre layer, formed chiefly by the retinal nerves and the visual cells (S.CE.).

The following details of the finer structure of the retina are taken from Hesse (1900) and Alexandrowicz (1927). The essential part of the retina consists of a layer of visual cells (Fig. 71, S.CE.) of elongated form, continued as rods (R.) projecting towards the centre of the eye. Each rod and sensory cell are connected by a meandering neurofibril (NF.) which forms a little knob at the inside end, while on the outside it enters the sensory nerve (N.O.G.) to the optic ganglion.

Internally the retina is bounded by the limiting membrane (L.M.) secreted by the limiting cells (L.C.) which

are connected to the membrane by fine protoplasmic threads (C.L.M.) passing between the rods. Between the rod zone and the visual cell zone there is another membrane (B.ME.), the basal membrane, which is secreted by connective tissue cells (C.CE.).

The retina is deeply pigmented with a dark brown pigment. This is situated mostly round the base of the rods (P.Z.) next to the external limiting membrane, and in another zone round the apex of the rods. There is a flow of pigment from the basal to the apical zone in bright light, which appears to have the function of regulating the amount of light reaching the visual cells.

The visual cells are continued mesially as the optic fibres or retinal nerves. These collect in bundles of about 300, each of which is surrounded by a thin sheath of connective tissue, continuous with the connective tissue separating the retina from the sclerotic, and which covers the latter as a thin membrane. The numerous arterial and venous blood-vessels supplying the retina run in this membrane. In addition it contains small bundles of muscle fibres called by Alexandrowicz the retinal muscles.

(*h*) ACCOMMODATION.

As the focal length of the lens cannot be altered, accommodation can only be achieved by alteration of the distance between the lens and the retina. Rather conflicting opinions have been put forward concerning the process and extent of accommodation. Most of the works referred to deal with cephalopod eyes in general, though *Sepia officinalis* has often been one of the chief types studied. Beer (1897) found that the eye at rest is adjusted for near vision, and that accommodation for long vision is achieved by the ciliary muscle, which draws the lens nearer the retina.

Hesse (1907) confirmed Beer but suggested that there is also accommodation for very near vision by moving the lens away from the retina. He was unable in his physiological experiments to establish exactly what this mechanism is. Hess (1909) on the other hand claimed that the cephalopod eye is hypometric, and by stimulation of the central nervous system he claims to have observed adjustment for near vision by moving the lens away from the retina. He attributed this to increased intrabulbular pressure, caused by the contraction of the ciliary muscle.

Alexandrowicz (1927) who used *Sepia officinalis* for his experiments, found in electrical experiments on fresh eyes isolated from the animal, that he could stimulate the ciliary muscle, causing accommodation for distant vision, and also that by stimulating the sclerotic muscles, he could cause accommodation for near vision. Alexandrowicz admits that one cannot say definitely that these movements, which can be induced in isolated eyes under electrical stimulus, do actually take place in the animal under normal conditions. He does however attribute the faculty of double accommodation to the Cephalopods, but he adds that of these two processes, accommodation for distant vision by means of the ciliary muscle has the greatest weight of evidence to support it. He says also that the muscles of the retina probably serve to keep the retina in place when the intrabulbular pressure varies during accommodation.

B. **Statocysts.**

The first mention of the so-called auditory organ of Cephalopods was made by Hunter (1782), but this was not accompanied by any description. The first detailed study of the statocysts was undertaken by Owsjannikow and Kowalevsky (1867). The more recent work of

Hamlyn-Harris (1903) contains both good figures and a detailed description of the statocysts of *Sepia*.

The statocysts (Fig. 79, SC.) are enclosed in the cartilage of the skull (Fig. 27, SC.C.). They are situated ventral to the visceral ganglion (Fig. 79, V.G.) and the posterior part of the pedal ganglion (P.). They lie close together separated only by a thin wall. Figures 68 and 69 show the two halves of the statocysts which have been cut through in the transverse dorso-ventral plane. The vesicle of each statocyst has a very irregular shape, caused by the projection into it of numerous protuberances (Fig. 69, P.S.) or ampullae as they are sometimes called. The sensory part of the organ consists of two regions, the macula statica (Fig. 68, M.ST.) and the crista statica (C.ST.). The former (with which are included two additional zones discovered by Hamlyn-Harris, who called them macula neglecta anterior, and macula neglecta posterior respectively, which are not lettered in Fig. 68) is situated in the dorsal anterior region. It consists of patches containing cylindrical ciliated cells. The crista statica is a little ridge, broken into three sections, which also contains similar ciliated sensory cells. In Figures 68 and 69 the crista appears to consist of more than three sections, but this is only because some of the protuberances overhang the ridge. Neither the macula nor the crista can be seen with the naked eye.

The vesicle is filled with liquid, and contains a large otolith (Fig. 70, (*a*) and (*b*)). This is made of calcareous needles held together by an organic base. It has the form of a little sphere, from which projects a broad flat piece. It is attached along one edge to the vesicle in the region of the macula. A small blind canal (Fig. 68, C.CA.) called Kölliker's canal after its discoverer, opens into the antero-lateral wall of the vesicle. This is the vestige of an invagination of the ectoderm which gives rise to the statocyst in the embryo.

For the description of the innervation of the statocysts reference should be made to the section on the nervous system (page 117). The statocysts are organs of balance.

C. **Olfactory Pits.** (Fig. 1., O.P.).

These are small ciliated pits situated posterior to the eyes. They are supplied by comparatively large nerves. Their position in front of the inhalent channels to the mantle suggest that their function is that of osphradia.

In addition to the above-mentioned organs of sense, the sucker zones of the arms and tentacles are to some extent sensory.

REPRODUCTIVE ORGANS.

A. **Female.**

The female reproductive organs consist of the ovary, the oviduct, and the nidamental glands. The ovary (Fig. 72, O.) hangs from the dorsal wall of the posterior part of the viscero-pericardial coelom (VP.). The eggs develop in delicate follicles, which are traversed by blood-vessels. When ripe they are released into the body cavity. Each egg is between 6 and 10 mm. in diameter. In a ripe female the whole of the posterior part of the viscero-pericardial coelom is packed with eggs.

The oviduct is a thin-walled tube situated on the left side. It is continuous with the cavity of the coelom, opening from it by a small aperture (A.OD.). The first part of the oviduct is quite wide and is attached to the ventral wall of the coelom. It gradually narrows as it travels anteriorly, and passes between the left branchial heart and the wall of the left side of the dorsal renal chamber of the renal sac.

At the distal end, where it leaves the visceral mass and projects into the mantle cavity, it has thick glandular walls of laminated structure, which constitutes the gland

of the oviduct (G.OD.). The function of this gland is to secrete the outer coat of the ova.

The nidamental glands are described in the section on the mantle cavity of the female (page 29). The process of fertilisation and egg-laying is described in the section on HABIT AND HABITAT (page 146).

B. **Male.**

The chief interest in the male reproductive organs of Cephalopods centres round the spermatophores, and the apparatus which manufactures them.

Swammerdam (published 1738) observed the spermatophores, and described how they burst when placed in water. But his understanding of the male generative organs was far from complete, and he was unable to determine if the spermatophores contained spermatozoa.

The first detailed account of the structure of the spermatophores was given by Needham (1745). Needham studied the spermatophores of the Calmary, and was aware that they contained the spermatozoa. A rather more precise description was published by Milne-Edwards in 1842. Chun (1905 and 1906), and Marchand (1906, 1907, and 1912) gave further details of the spermatophore-producing apparatus, and of the spermatophores themselves. Blanquaert (1925) gives a very careful account, both of the spermatophores and of their manufacture. Blanquaert's work was done on *Sepia*, and the description given here is based on his memoir.

(*a*) TESTIS.

The testis (Fig. 20, TE.) is a large compact body which is attached to the postero-dorsal wall of the viscero-pericardial coelom (VP.), and occupies a position corresponding to that of the ovary in the female. It opens into the coelom by an aperture (O.T.) situated on its ventral surface.

(*b*) SPERMATOPHORE-PRODUCING APPARATUS.

The male genital duct is, like that of the female, continuous with the coelom, and similarly placed, but it is larger, and its structure is very much more complex. It lies on the left side of the body, and the genital orifice which opens into the mantle cavity, lies at the end of a fleshy protuberance (part of Needham's pocket, Fig. 5, M.D.) projecting anteriorly from near the base of the left branchia.

[DISSECTION :—*Remove the entire male genital duct together with that part of the coelomic wall to which it is attached, from the body of the animal. Open the genital sac* (Fig. 74, G.S.). *After identifying the parts which can be seen in this sac* (*compare with* Fig. 74) *free the individual parts so that they can be arranged as in* Fig. 75.]

The spermatophore-producing apparatus is enclosed in a thin-walled genital sac (Fig. 74, G.S.), which is not in communication with the coelom. This sac opens into the mantle cavity through a little slit (Figs. 5, 74, A.G.S.) on the outside of the fleshy protuberance at the end of which the genital orifice is situated. According to Chun (1905) the genital sac is not a diverticulum of the coelom.

The genital duct commences on the ventral wall of the posterior part of the coelom. The opening (Fig. 74, A.P.D.C.) in the coelom leads into a slender tube, the proximal deferent canal (Figs. 74, 75, P.D.C.), which varies in length from 5 to 10 cms. according to the size of the specimen. This tube is very much convoluted and packed into a tangled mass. The anterior half of it cannot be seen in Figure 74 as it is obscured. This tube does not lie in the genital sac, but is bound to the wall of the coelom by a membrane.

At its distal end the proximal canal opens into a reniform seminal vesicle I (Fig. 75, S.VE., I.). This leads to seminal

vesicle II, which consists of three parts, one of them spherical on the outside (C.S.VE., II.), another almond-shaped (A.S.VE, II.), while the third consists of a cedilla-shaped appendage (A.A.S.) of the almond-shaped part. Seminal vesicle III (S.VE., III.), is a large structure, the canal of which is crescent-shaped in cross-section (Fig. 76, S.VE.,III.), through most of the cavity being occupied by a projection from the side of its wall. The next part was called the prostate by earlier authors, but has been re-named the accessory gland (Figs. 74, 75, 76, A.G.). It has thick glandular walls enclosing a large cavity. The accessory gland is entered from seminal vesicle III. by a very narrow passage. A slender canal, called the ciliated canal (Figs. 75, 76, CI.C.) is given off from this passage, and opens by a funnel-like expansion into the genital sac.

The duct which leads out of the accessory gland travels into a structure of complicated internal form, called the appendage of the accessory gland (Figs. 74, 75, 76, A.A.G.). This is shown in section in Figure 76. The latter leads by a slender tube, the distal deferent canal (Figs. 75, 76, D.D.C.) to the posterior end of Needham's pocket (Figs. 74, 75, N.P.) at the end of which the genital orifice is situated.

(*c*) STRUCTURE OF SPERMATOPHORES. (Figs. 77, 78).

Each spermatophore consists of a little tube, either straight or slightly curved, and between 10 and 15 mm. in length. Its aboral extremity is dome-shaped, while the other, called the oral end, terminates in a slender filament (Fig. 77, T.F.).

The internal parts of the spermatophore are enclosed in a sheath or tunic (Figs. 77, 78, T.S.) which contains the sperm reservoir (Fig. 77, SP.R.) and a very intricately constructed ejaculatory or explosive apparatus (Fig. 77, SA.S., HO. and TW.S.). The sperm reservoir is attached to the explosive apparatus by a slender ligament (Fig. 77, CON.);

otherwise it lies quite freely within the tunic. The tunic is not of constant thickness, but is thinner at the oral end.

The sperm reservoir is an elongated cylinder of uniform diameter. It appears under the microscope to have a very close and regular spiral structure, though its outer surface is quite smooth. The ejaculatory apparatus consists of two parts, the sac (Fig. 77, SA.S.) and the horn (HO.). There is no distinct separation between these two parts, but the beginning of the horn is marked by a groove. The horn, together with the three membranes which surround it, form at the oral end of the spermatophore the terminal twist (TW.S.).

The external membrane (Figs. 77, 78, E.M.) is continuous with the connective (Fig. 77, CON.) which attaches the sperm reservoir to it. The middle membrane (Fig. 78, MI.M.) is attached to the oral end of the sac. It bears little folds or pleats very close together which give the impression of very regular annulation. The internal membrane (I.M.) is thick, smooth and quite transparent.

(*d*) MANUFACTURE OF SPERMATOPHORES.

Except for the spermatozoa themselves, the entire spermatophore is made from secreted products. The proximal efferent canal is always packed with spermatozoa, and Needham's pocket is the storage place for the completed spermatophores. The actual manufacture takes place in the intervening part of the duct. The whole of this duct is ciliated, and shows very pronounced differentiation of its epithelium in different regions, without usually showing any transition cells. It is a difficult problem to explain how this apparatus is organised to produce such intricate objects as the spermatophores, with such constancy of form and dimensions. It appears that this result is achieved through the combined effects of the anatomy of the apparatus, the rhythmical movements of

the cilia, and the co-ordination of the secretion of the different parts of the complicated epithelium which lines the passage of the apparatus.

1. Formation of sperm reservoir. (Fig 77, SP.R.).

From the time of their entry into the seminal vesicle I. the spermatozoa are embedded in the viscous substance secreted by the walls of the latter. This mass is conducted along a spout-like groove to the cylindrical opening into seminal vesicle II. Additional secretion from seminal vesicle I. arrives at the opening from two sides. The mass of embedded sperms is surrounded by this and conveyed through a short circular corridor leading to seminal vesicle II. It is propelled in a spiral way which gives the sperm reservoir its spiral appearance. The rudiment of the connective (Fig. 77, CON.) is also formed here.

2. Formation of central axis of ejaculatory apparatus. (Figs. 77, 78, SA.S. and HO.).

The sperm reservoir travels along a groove in seminal vesicle II. At a certain point the secretory part of this vesicle is stimulated. The secretions reach the groove at two separate times. First the sac is formed with a spiral rolling movement, and a little later, the central part of the horn.

3. Formation of membranes. (Fig. 78, I.M., MI.M. and E.M.), and connective (Fig. 77, CON.).

The internal, middle and external membranes are formed in the proximal part of seminal vesicle III. The connective is completed, and at this stage the sperm reservoir is definitely attached to the ejaculatory apparatus.

4. Formation of sheath or tunic. (Figs. 77, 78, T.S.).

The sheath is formed of a single substance secreted throughout the whole length of seminal vesicle III.

5. Formation of twist and filament. (Fig. 77, TW.S. and T.F.).

The twisting of the terminal part of the horn is achieved in the appendage of the accessory gland (Fig. 76, A.A.G.), the twisted part being covered by a secretion which prevents it from untwisting. The terminal filament is formed by a little tubular gland which opens into the beginning of the distal deferent canal (D.D.C.). The completed spermatophores pass along the distal deferent canal to be stored in Needham's pocket. Both in the accessory gland and at the entrance into Needham's pocket a reversal of the direction of the spermatophores takes place.

The function of the ciliated canal (Figs. 75, 76, CI.C.) is to enable surplus secretions to be removed from the apparatus which produces the spermatophores. These secretions after passing into the genital sac (Fig. 74, G.S.) can escape to the mantle cavity *via* the aperture (A.G.S.).

(*e*) EXPLOSION OF SPERMATOPHORES.

While in Needham's pocket the spermatophores remain inactive, but when transferred to a drop of water the spring mechanism uncoils, bursting the enclosing sheath and liberating the sperm reservoir. The latter then swells and bursts, thus allowing the spermatozoa to escape. These, which remain passive within the sperm reservoir, become active in sea water. The spermatophores retain their power of exploding for some time after the animal is killed.

DUCTLESS GLANDS.

Under this heading are included three glands, whose function has long been a matter of controversy.

1. PERICARDIAL GLANDS. (Fig. 20, P.GL.).

These are compact bodies, which lie in the pockets of the viscero-pericardial coelom in which the branchial hearts

(B.H.) are situated. They are attached to the latter. Kestner (1931) who performed physiological experiments on *Sepia* in connection with these glands, expresses the view that they are probably endocrine in function.

2. BRANCHIAL GLANDS. (Figs. 25, 54, 81, B.GL.).

These glands lie along the dorsal sides of the axes of the branchiae. Like the pericardial glands they have a good blood supply. Hutchinson (1928) suggests that it is possible they may be endocrine in function, and adds that no case is known of an endocrine gland in Invertebrates, but that, if they do occur, it is in the Cephalopods, whose organisation is in many respects equal to that of the lower Vertebrates, that one would expect to find them.

3. WHITE BODIES. (Figs. 59, 67, W.B.).

The white bodies lie round the optic ganglia, and also round the cerebral ganglion. They are developed from the ectoderm in close connection with the nervous system. Noel and Jullien (1933), who included *Sepia* in their work, say they are definitely leucocyte-forming glands.

HABITS AND HABITAT.

Although the cuttlefish spends part of its life in comparatively shallow coastal waters, part is also spent in deeper regions. Cuénot's work (1916) indicates that seasonal migrations are undertaken in connection with spawning. He claims that among the three varieties of the common cuttlefish, *Sepia officinalis officinalis*, *Sepia officinalis fillioux*i and *Sepia officinalis fischeri*, originally distinguished by Lafont, in 1869, on the basis of small variations in the shell of specimens caught in the gulf of Arcachon, there is a sharp racial distinction, though they cannot be regarded as distinct species. In this district variety *officinalis* live in shallow waters in the summer while their reproductive organs are still immature, and

return to deeper waters at the approach of winter to lay their eggs in places unknown. *Fillioux*i and *fischeri* on the other hand migrate to shallow waters in early spring and summer to spawn. *Fillioux*i reaches sexual maturity between February and April, and *fischeri* between April and August. Although Cuénot states that it is certain these three forms present an almost complete physiological separation, he suggests that in the case of shells which are difficult to classify, the explanation lies in the occasional interbreeding, made possible by the slight overlapping of the periods of sexual maturity among the three varieties. Experiments in tanks have shown that there is no psychic separation. In addition to the regular migration of the three varieties of *Sepia officinalis* described by Cuénot, Grimpe has observed a certain periodicity in the numbers of *Sepia officinalis* in the North Sea, for it appears that in some years this species is much more abundant in these waters than at other times.

When not swimming *Sepia* lives on the sea bed, and likes either *Zostera* beds or a sandy bottom where it can bury itself. According to Kühn and Heberdey, *Sepias* placed in tanks without sand are restless and excited, although if there is a little sand, but not enough for them to bury themselves in, they will lie quite peacefully on the bottom. Except in the act of capturing prey the tentacles are retracted and the arms held with their tips together in a sort of cone (Fig. 1).

The cuttlefish is quite a good swimmer, and can propel itself through the water both by its fins and by the action of its funnel. When the fins are used, undulations pass along them, starting either from the anterior or from the posterior end, according to the direction in which the animal intends to go. In this way it can swim either forwards or backwards. Sometimes the two fins work independently, and occasionally it uses one of them for

achieving a sideways motion. When using its fins for swimming, the cuttlefish assists the motion by pointing the mouth of the funnel in such a direction that the water leaves in the opposite direction to that in which it is travelling. The funnel is often pointed sideways to assist in changing direction.

It can also move backwards with swift darting movements by violent ejection of water from the funnel, caused by powerful contraction of the muscular wall of the mantle. When it swims in this way the fins are folded against the ventral sides of the body, giving a stream-lined effect. This method of locomotion is usually adopted when it is alarmed, and when this is the case a cloud of black ink is ejected into the water which leaves the funnel. Originally it was thought that the ink formed a " smoke " screen behind which the animal retreated. Recent observations, however, suggest that the jet of ink, when shot out, does not diffuse rapidly, but persists as a definite object in the water, and serves as a dummy to engage the attention of the enemy, while the cuttlefish changes its colour so that it may be as nearly invisible as possible, and darts off in another direction.

The cuttlefish adapts its colouration to its surroundings by means of chromatophores and iridocytes which lie in the dermis. Although its powers in this respect are not equal to those of the plaice when subjected to critical tests, under normal conditions it can mimic its surroundings very effectively. Among the colours it cannot assume are pure red and blue. When irritated, and more especially during copulation, a dazzling display of colour takes place, and the whole back of the animal exhibits zebra-like stripings.

In common with many other Cephalopods *Sepia* may exhibit luminescence. Girod (1882), in describing how he obtained specimens for his researches off the coast of

Roscoff, says that between the months of February and March, which is the period of fecundation, the female swims at the surface at night, emitting quite a bright luminescence. Males lurking among the rocks at the bottom of the sea rush on to her like luminous arrows.

Sepia's food consists chiefly of crabs, small whiting, shrimps and prawns. It captures the latter by means of its tentacles which are shot out together with lightning speed, acting like a pair of tongs (Fig. 2). They can be extended to well over the total length of the animal itself.

Data concerning the enemies of the cuttlefish are lacking, but it is certainly preyed upon to some extent by large fishes. It can be caught in various ways, by the drag net, the seine, and by hand line. If a ripe female is attached to a fixed line by the posterior end of the shell and left in shallow water, males are attracted from great distances. In some countries a piece of cork is cut roughly the shape of a cuttlefish and a piece of mirror attached to it. When this is towed behind a boat at night the mirror reflects the light of a flare in the boat, and males mistaking it for a female are attracted and can easily be caught.

The cuttlefish, together with various other Cephalopods, have been a source of food in the Mediterranean basin since early times. Swammerdam records that *Sepia* was eaten in Holland in the seventeenth century, sometimes cooked, but more often after being dried in the open air. Cephalopods are not generally used as food by the Anglo-Saxon race, though the mantle of *Sepia* is sometimes fried and eaten by fishermen. *Sepia* is, however, consumed in much greater quantities in other parts of the world. In Naples the flesh is not so well esteemed as that of *Octopus* and *Loligo*, but it is obtained and sold in great quantities, and additional supplies are obtained from the Adriatic and the gulf of Manfredonia.

Copulation and egg-laying take place quite readily in captivity. The following account is taken from Grimpe (1926). In the type of aquarium used, *Sepia officinalis* was maintained with reasonably natural behaviour. Ripe females were introduced to males, and pairing commenced. Typical colour effects appeared, and the arms were expanded and united in a close amplexus for from two to five minutes, after which the female slowly freed itself. During copulation the male placed spermatophores on the bursa copulatrix of the female with the aid of the left hectocotylised arm, and with the assistance also apparently of the right ventral arm, though it was impossible to see exactly what was happening. Union was repeated several times in a few days, and a certain amount of monogamy was observed. Meanwhile egg deposition took place. Eggs emerged one by one *via* the funnel and the bursa where fertilisation presumably takes place. The secretion of the nidamental glands and ink gland was poured on the egg (this secretion soon hardens to a tough consistency) which was then attached to a suitable place. The female used the ventral arms for this. After deposition of each egg the funnel was flushed.

The above account does not explain how the male gets hold of the spermatophores in order to place them on the bursa of the female. Observations by Bert (1867) may throw light on this. Bert was not aware of the location of the bursa, and states that in his experiments he failed to find any spermatophores in the mantle cavity of the female after copulation. However, when he interrupted copulation by separating two individuals he found that the hectocotylised arm of the male was inside its own mantle cavity. It seems probable from this observation that the male extracts the spermatophores from its mantle cavity with this arm.

A further point which requires elucidation is how the spermatozoa are stored after the spermatophores have been attached to the bursa, as the spermatophores burst quite soon after coming in contact with sea water. This problem has not been studied in the case of *Sepia*, but it has been investigated in *Loligo vulgaris*, in which the spermatophores are deposited in a corresponding place during copulation. According to van Oordt (1938) there is in *Loligo* a depression on the inner side of the ventral part of the buccal membrane as the buccal funnel is often called. This depression evidently corresponds to that which in the case of *Sepia* has been called the bursa copulatrix, and as in *Sepia*, the spermatophores are deposited in it during copulation. Within this depression lies a small mamma-like structure, with a distinct nipple. The spermatozoa reach this spermatheca probably by chemical attraction, and are stored there in an inactive state.

It is probable that a similar storage structure is present within the bursa copulatrix of *Sepia*, but for lack of suitable material it was not possible to confirm this.

Jullien (1926) describes various forms in which the eggs were deposited by *Sepias* in captivity. The animals were kept in wicker enclosures in shallow water near Toulon. Sometimes the eggs were laid in the characteristic form of black "sea grapes," each egg being attached by a little stalk to a twig of a marine plant, and each bunch consisting of 260 to 300 eggs being completed in two to three days, by *Sepias* which had been captive and fasting for two weeks. At other times they were laid closely packed together in a single layer. White "sea grapes" were also laid.

The eggs develop quite normally in tanks, and this, combined with the readiness with which *Sepia officinalis* will spawn in captivity, makes it the most suitable Cephalopod type for embryological studies which occurs in European waters.

APPENDIX.

A. Size of Specimens.

For dissection, the larger the specimens the better. Usually mature specimens obtained round the British coasts vary in size from 11 to 18 inches, measured from the tip of the arms (not the tentacles) to the posterior end. Owing to the seasonal migrations of the various varieties, the specimens usually caught in the summer are half-grown and sexually immature. Large specimens are brought in chiefly in the autumn and early spring.

B. Preservation of Specimens.

Formalin is a very good preservative for general dissections. The eyes and brain should first be injected with 10 per cent. formalin, and then the whole specimen should be placed in 4 per cent. formalin. If a stronger solution is used, the specimens become inconveniently hardened. In this solution the specimens will remain in good condition for several years, but the funnel glands and the delicate filaments of the branchiae usually degenerate within a few months.

Grimpe (1913) states that he placed his specimens (*Sepia* and *Octopus*) in 4 per cent. formalin for 60 to 80 hours, and then, after carefully washing them in 30 per cent. alcohol, transferred them to 80 per cent. alcohol.

The dissection of the nervous system is greatly facilitated if the formalin material is kept in water for many weeks, the water being changed frequently. By this method, which is recommended by Hillig (1912), the flesh becomes macerated, so that the muscles can be easily removed from the more resistant nerves. But more important still, the membranes in which some of the nerves run tend to become transparent after long soaking in water, while the nerves themselves hardly change, so that the latter can be more easily seen.

The following chromic acid method of preservation is, according to Hillig, specially suitable for the preparation of the peripheral nervous system. The freshly caught Cephalopod has its mantle slit open and a little 4 per cent. formalin added to the sea water in which it has been placed. After a few hours it has become fairly hard. It is then washed in water, and placed for two days in a dilute solution of chromic-acetic acid of strength 9 parts water to 1 part solute. The solute is made up as follows :—

50 parts acetic acid (glacial).
10 parts chromic acid.
40 parts distilled water.

After fixation with chromic-acetic acid solution the specimens are kept for from five to eight days in water, and then transferred to 70 per cent. alcohol, which should be changed several times. By this method the muscles are noticeably loosened, and coloured slightly green, whilst the nerves appear yellowish. The method is not suitable for dissection of the central nervous system, which decomposes under this treatment.

C. Dissection.

All dissection should be done under water. Large pie-dishes, at least 3½ inches deep, and filled to a depth of ½ inch with wax make quite suitable dissecting dishes. For the dissection of the arteries and veins injection is essential.

D. Injection of Circulatory System.

Provided fairly fresh specimens are used, both the arteries and veins inject very well. Owing to the thinness of the walls of the auricles in the arterial system, and of all the vessels of the venous, only a moderate pressure should be exerted. It is possible to make satisfactory injections by the use of an ordinary hypodermic syringe alone, but a simple apparatus such as that illustrated and

described by Grimpe (1913), which is slightly modified from Sahaefer, greatly facilitates the operation.

Hot injection masses are impracticable, as the tissues of *Sepia* will not withstand the preliminary heating up of the specimen. Starch can be used though it is inclined to deposit in the large vessels. Gelatine-Glycerin cold injection mass is very convenient as it flows quite freely. The only drawback is, that, in order to fix the gelatine, it is necessary to place the injected animal in 10 per cent. formalin, which causes it to become rather hard.

Preparation of Gelatine-Glycerin cold injection mass.

Stock gelatine.

Soak best white gelatine in water for 12 hours; then pour off the excess of water, and melt the residue.

Soluble Prussian blue injection fluid.

A. Potassium ferrocyanide 4 per cent. (aqueous sol.), 500 ccs.

B. Iron perchloride 2 per cent. (aqueous sol.), 500 ccs.

Add *B* slowly to *A*, stirring all the time. Allow to stand overnight. Syphon off the supernatant liquor. Transfer the precipitate to a filter paper, and wash repeatedly with small quantities of water till the filtrate is deep blue. Dissolve the whole precipitate in 1,000 ccs. of water.

Injection mass.

Stock gelatine melted	... 60 gms.
Potassium iodide	... 6 gms.
Glycerine	... 60 ccs.
Soluble Prussian blue injection fluid ...	...240 ccs.

When Prussian blue is used as the colouring matter, the colouring is very intense, so that even the smallest vessels show up conspicuously. Other colouring matters can be added in place of the blue, but most other colours do not show up the vessels as well as the blue.

Injection of arteries.

The arteries are most conveniently injected by inserting the needle into the efferent branchial vessel about half-way along the branchia. This vessel runs along the mid-ventral line of the branchia just beneath a little muscular tissue.

Injection of veins.

Insert the needle laterally between the outer lip of the buccal mass and the buccal funnel, and inject into the peri-buccal sinus. A large volume of liquid is required to fill the veins. If it is attempted to inject from the cephalic vein it is very difficult to get the injection to flow into the head as it has to be forced the wrong way through the valves guarding the openings of the veins which enter the cephalic vein from the head.

E. Preparation of Chromatophores.

The following practical details are taken from Bozler (1928). For morphological work it is best to take the material from the living animal. *Loligo vulgaris* is the most suitable species as its skin is very transparent, and the chromatophores are larger than those of *Sepia* and *Octopus*. The skin is prepared for examination by stripping off a piece and stretching it on a little cork frame, so that no displacement can occur through the contraction of the skin muscles. The layer of the skin which covers the layer in which the chromatophores lie should be removed. The preparation made in this way can be covered with a cover glass and examined under the microscope.

For histological work fix the whole body of the Cephalopod in Zenker's solution. This prevents the skin from shrinking by muscular contraction. Then strip off a small piece of the skin and stain with iron haematoxylin.

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EXPLANATION OF PLATES

Reference Letters.

A.1., 2., 3., 4. = Arms 1-4.
A.A.F. = Anterior adductor muscle of funnel.
A.A.G. = Appendage of accessory gland.
A.A.N.G. = Apertures of accessory nidamental glands.
A.A.S. = Appendage of seminal vesicle II.
A.A.V. = Anterior azygos vein.
A.B. = Anterior ctenidia or branchia.
A.B.G. = Anterior branchial ganglion.
A.C.A. = Anterior cephalic artery.
A.C.C. = Attachment of single lamina to columella of caecum.
AC.N.G. = Accessory nidamental gland.
A.C.V. = Anterior cephalic vein.
A.D.C. = Cut surface where retractor muscle of head is attached to diaphragm cartilage.
A.F. = Anterior end of fin.
A.F.A. = Anterior fin artery.
A.FI.V. = Anterior fin vein.
A.F.N. = Anterior funnel nerve.
A.FU.A. = Anterior funnel artery.
A.F.V. = Anterior funnel vein.
A.G. = Accessory gland.
A.G.A. = Anterior accessory genital artery.
A.G.S. = Opening of genital sac into mantle cavity.
A.G.V. = Anterior accessory genital vein.
A.H.R.N. = Anterior nerve of retractor muscle of head.
A.L.G. = Adductor ligament of genital duct.
AM. = Ampulla of inksac.
A.M. = Anterior chamber of mantle cavity.
A.M.A. = Anterior mantle artery.
A.M.V. = Anterior mantle vein.
AN. = Anus.
A.N.G. = Artery of nidamental gland.
AN.V. = Anal valves.
A.O.A. = Anterior oesophageal artery.
A.OD. = Aperture of oviduct in viscero-pericardial coelom.
A.O.M.N. = Anterior oculomotor nerve.
A.P.D.C. = Aperture in coelom of proximal deferent canal.
A.P.V. = Anterior vein to pancreatic appendages.
A.R. = Adductor muscle of radula.
A.R.A. = Anterior renal artery.
A.R.B. = Axial part of retractor muscle of branchia.
A.RE. = Adductor muscle of rectum.
A.S.G. = Anterior salivary gland.
A.S.I. = Anterior sphincter muscle of inksac.
A.SU. = Attachment flange of sucker.
A.S.VE.II. = Almond-shaped part of seminal vesicle II.
AU. = Auricle.
A.V. = Afferent branchial vessel.
A.V.A. = Aboral vein of arm.
A.V.C. = Anterior visceral commissure.
A.VP.C. = Aperture of viscero-pericardial coelom.
B. = Branchia.
B.A. = Buccal artery.
B.A.M.A. = Branches of anterior mantle artery to mantle wall.
B.B.C. = Brachio-buccal commissure.
B.C. = Bursa copulatrix.
B.CA. = Blood capillary.
B.CR. = Brown chromatophore.
B.F. = Buccal funnel.
B.G. = Buccal ganglion.
B.GA. = Branchial ganglion.
B.GL. = Branchial gland.
B.H. = Branchial heart.
B.L. = Branchial membrane and ligament.
B.M. = Buccal mass.
B.ME. = Basal membrane of retina.
B.N. = Brachial nerve.
B.N.I., 2., 3., 4. = Brachial nerves of arms 1-4.
B.P. = Buccal pocket.

B.P.M.A. = Branches of posterior mantle artery to mantle wall.
B.P.N. = Nerves of buccal pillars.
BR. = Bridge between orbital cartilages of skull.
BR.A. = Brachial artery.
BR.A.1., 2., 3., 4. = Brachial arteries of arms 1-4.
BR.C. = Brachial cartilage.
BR.CA. = Branchial cartilage.
BR.G. = Brachial ganglion.
BR.M. = Branchial membrane attaching branchial gland to mantle wall.
BR.N. = Branchial nerve.
BR.V. = Main brachial vein.

C. = Cerebral ganglion.
CA. = Spiral caecum.
CAE.N. = Nerve of caecum.
CA.N. = Cardiac nerve.
C.B.C. = Cerebro-brachial commissure.
C.B.S. = Superior inferior buccal commissure.
C.BU.C. = Cerebro-buccal commissure.
C.C. = Cephalic cartilage of skull.
C.CA. = Kölliker's canal.
C.CE. = Connective tissue cell.
C.D.C. = Cut wall of dorsal chamber of renal sac.
CE.A. = Cephalic artery
CE.C. = Cerebral cartilage of skull.
C.E.M. = Cut edge of muscle.
CE.V. = Cephalic vein.
C.F. = Cut wall of funnel.
CI.AP. = Circumoral appendages.
CI.C. = Ciliated canal.
C.I.G. = Clear centre of ink gland.
CI.M. = Ciliary muscle of eye.
C.L. = Muscular capsule of digestive glands.
C.L.C. = Cut surface of lateral commissure.
C.L.M. = Protoplasmic connection between limiting cell and limiting membrane.
C.M. = Cut wall of mantle.
C.M.S. = Circular muscle of stomach
C.N. = Collar muscle nerve.
CO. = Coelom.
C.O.G. = Cut surface of optic ganglion.
CON. = Connective of spermatophore.
C.O.N. = Cut surface of optic nerve.
COR. = Cornea of eye.
C.O.S. = Communication of optic sinus with vein from head sinuses to cephalic vein.
C.PH. = Chambers of phragmocone.
CR. = Crop.
C.RO. = Calcareous rostrum.
C.S. = Cut edge of skin.
C.SH. = Calcareous part of shell margin.
C.S.N. = Nerve of crista statica of statocyst.
C.ST. = Crista statica.
C.SU. = Circular muscle of sucker.
C.S.VE. II. = Circular mass of seminal vesicle II.
C.T. = Connective tissue.
C.V.C. = Posterior communication between the two ventral chambers of renal sac.
C.VP. = Cut wall of visceropericardial coelom.
C.V.R. = Cut wall of ventral chamber of renal sac.

D.A.S. = Duct of anterior salivary gland.
D.C. = Dorsal chamber of renal sac.
D.CA. = Diaphragm cartilage.
D.D.C. = Distal deferent canal.
D.F.M. = Dorso-lateral fin muscle.
D.F.ME. = Dorso-lateral fin membrane.
D.G.A. = Dorsal gastric artery.
D.H.V. = Dorsal head vein.
D.I. = Duct of inksac.
D.IS. = Dorsal surface of inksac.
D.J. = Dorsal jaw.
D.L. = Duct of digestive gland.
D.O. = Duct from exterior to orbit.
D.O.A. = Dorsal orbital artery.
DO.CA. = Dorsal cartilage.
D.PH. = Dorsal part of phragmocone.
D.S.G. = Duct of posterior salivary glands.
D.SH. = Hard calcareous dorsal surface of shell.
D.S.N. = Nerves to skin of dorsal surface.
D.T. = Dorsal sucker margin of tentacle head.

E. = Epidermis.
E.A. = External argentea of eye.
E.A.M. = Extrabrachial muscle zone of arm.
E.B. = Epithelial body of eye.

E.C. = Equatorial cartilage of eye.
EL. = Eyelid.
E.M. = External membrane of spermatophore.
E.P.N. = Emergence of pallial and posterior head retractor nerves.
E.S.E. = Exhalent siphon of funnel.
E.SH. = Embryonic shell.
E.T.M. = Extrabrachial muscle zone of tentacle.
E.V. = Efferent branchial vessel.
E.V.N. = Emergence of visceral nerve.
EYE. = Eye.
F. = Funnel.
F.A.F. = Foramen of anterior funnel nerve.
F.A.H. = Foramen of anterior head retractor nerve.
F.A.M.V. = Factors from mantle wall of anterior mantle vein.
F.A.O. = Foramen of anterior oculomotor nerve.
F.A.V. = Foramen in diaphragm cartilage of anterior azygos vein.
F.C. = Funnel cartilage.
F.C.N. = Foramen of collar nerve.
F.D. = Female genital duct.
F.G. = Funnel gland (Organ of Verrill).
FI. = Swimming fin.
FI.C. = Fin cartilage.
F.I.P. = Foramen of inferior posterior ophthalmic nerve.
F.M. = Free margin of mantle.
F.MA. = Foramen magnum of cephalic cartilage.
F.N. = Nerves of fin.
F.O.B. = Foramen through membrane, communicating between peri-oesophageal and peri-buccal blood sinuses.
F.O.N. = Foramen of olfactory nerve.
FOOT. = Foot.
F.O.V. = Foramen in skull of vein from head sinuses to cephalic vein.
F.P.F. = Foramen of posterior funnel nerve.
F.P.N. = Foramen of postorbital nerve.
F.R.N. = Foramina of retinal nerves through sclerotic cartilage.
F.S. = "Fork" of ventral part of phragmocone.
F.SH. = Free margin of shell.
F.S.P. = Foramen of superior posterior ophthalmic nerve.
F.T. = Fibrous connective tissue.
F.V. = Funnel valve.
F.V.E. = Foramen in skull of ophthalmic vein from eye sinus to cephalic vein.
G.A. = Genital artery.
G.A.V. = Genital artery and vein.
G.C.S. = Groove from region of opening of duct of digestive glands into caecum, to region of stomach.
GD. = Genital duct.
G.D.N. = Nerve of genital duct.
G.G. = Gastric ganglion.
G.J. = Groove into which dosal jaw fits.
G.N.C. = Groove of nuchal cartilage.
GO. = Gonad.
G.O. = Groove leading to oesophagus between palatine lobes of buccal mass.
G.OD. = Glands of oviduct.
G.OR. = Genital orifice.
G.P.B. = Groove separating pedal and brachial ganglia.
G.S. = Genital sac.
G.T. = Glandular part of tongue.
G.V. = Genital vein.
G.V.P. = Groove separating visceral and pedal ganglia.
H. = Heart.
H.A. = Hepatic artery.
H.C. = Horseshoe cartilage.
HE. = Head.
HE.A. = Arteries supplying dorsal part of head.
HO. = Horn of spermatophore.
H.OES. = Horny lining of oesophagus.
H.R. = Horny ring of sucker.
H.R.M. = Horny covering of anterior part of radula membrane, from which radula teeth project.
H.RO. = Horny tissue in region of rostrum.
H.S. = Horny lining of stomach.
H.SH. = Horny part of shell margin.
I. = Iridocyte.

I.A. = Intestinal artery.
I.A.N. = Inferior antorbital nerves.
I.A.O.N. = Inferior anterior ophthalmic nerve.
IB.C. = Interbrachial commissure.
I.B.G. = Inferior buccal ganglion.
I.C.F. = Inner collar muscle of funnel.
I.G. = Ink gland.
I.L. = Inner circular lip.
I.L.S. = Indentation of digestive gland where it rests against posterior salivary gland.
I.M. = Internal membrane of spermatophore.
IN. = Intestine.
I.P.O.N. = Inferior posterior ophthalmic nerve.
IR. = Iris.
IR.A. = Branch of ophthalmic artery to iris.
IS. = Inksac.
IS.A. = Inksac artery.
IS.A.V. = Inksac artery and vein.
I.SI. = Inhalent siphon of funnel.
IS.N. = Inksac nerve.
IS.V. = Inksac vein.
I.W. = Interbrachial webbing.

L. = Digestive gland or liver.
L.A.F. = Lateral adductor muscle of funnel.
L.B.V. = Lateral brachial vein.
L.C. = Limiting cell which secretes limiting membrane of retina.
L.CA. = Laminae of caecum.
L.CH. = Living chamber of shell.
L.D.N. = Nerve of duct of digestive gland.
LE. = Lens.
L.F.O. = Lateral ligament contributing to formation of foramen of optic nerve.
LI.V.D. = Posterior limit of communication between right ventral renal chamber and dorsal renal chamber.
L.M. = Limiting membrane of retina.
L.M.A. = Longitudinal muscle zone of arm.
L.M.B. = Lateral retractor muscle of buccal mass.
L.M.T. = Longitudinal muscle zone of tentacle.
L.M.V. = Left mesenteric vein.
L.P. = Lateral pocket or valve of funnel.
L.R.A. = Lateral ridge of ventral arm.
L.S. = Last septum of dorsal part of phragmocone.
L.V.D. = Lumen between ventral and dorsal chambers of renal sac.

M. = Mantle.
M.A. I. = Anterior oculomotor muscle I.
M.A.C. I. = Anterior conjunctive oculomotor muscle I.
M.A.C. II. = Anterior conjunctive oculomotor muscle II.
M.A.V. = Median mantle artery and vein.
M.BR. = Muscle of branchia.
M.C. = Mantle cartilage.
M.CA. = Mantle cavity
M.CE.V. = Muscular chamber of cephalic vein.
M.CR. = Muscle of chromatophore.
M.D. = Male genital duct.
M.F. = Mantle fold.
M.H.V. = Median (paired) hepatic vein.
M.I. I. = Inferior oculomotor muscle I.
M.I. II. = Inferior oculomotor muscle II.
MI.M. = Middle membrane of spermatophore.
M.J. = Muscle of jaw.
M.M. = Muscular secondary mantle.
M.M.A. = Median mantle artery.
M.M.V. = Median mantle vein.
MO. = Mouth.
M.O.L. = Membrane continuous with outer lip, and lining cone enclosing buccal mass.
M.P. I. = Posterior oculomotor muscle I.
M.P. II. = Posterior oculomotor muscle II.
M.P.B. = Membrane enclosing posterior part of brain.
M.R.B. = Marginal part of retractor muscle of branchia.
M.R.F. = Membrane attaching respiratory filament of branchia to axial part of branchial muscle.
M.S. = Mucous-secreting surface of hectocotylised arm.
M.SH. = Margin of shell.
M.S.N. = Nerve of macula statica.
M.ST. = Macula statica.
M.SU. I. = Superior oculomotor muscle I.

M.SU. II. = Superior oculomotor muscle II.
M.SU. III. = Superior oculomotor muscle III.
M.S.V. = Median shell sac vein.
M.T. = Muscular central part of tongue.
M.TR. I. = Trochlear oculomotor muscle I.
M.TR. II = Trochlear oculomotor muscle II.
M.TR. III = Trochlear oculomotor muscle III.
M.V.A. = Muscle of ventral arm.

N. = Nidamental gland.
N.A. = Aperture of nidamental gland.
N.C. = Nuchal cartilage.
N.CR. = Nucleus of pigment cell of chromatophore.
NF. = Neurofibril of rod of retina.
N.G.N. = Nerve of nidamental glands (in female).
N.M.CR. = Nucleus of chromatophore muscle.
N.O.G. = Nerves to optic ganglion.
N.P. = Needham's pocket.
N.R.F. = Nerve of retractor muscle of funnel.
N.SU. = Nerve of sucker.

O. = Ovary.
O.A. = Ophthalmic artery.
O.A.S. = Opening of anterior salivary gland.
O.C. = Orbital cartilage of skull.
O.C.A. = Artery to outer collar muscle.
O.C.F. = Outer collar muscle of funnel.
O.CR. = Orange chromatophore.
OD. = Odontophore.
O.D.C. = Outline of dorsal chamber of renal sac.
O.D.L. = Opening of duct of digestive glands into caecum.
OES. = Oesophagus.
O.F.M. = Origin of retractor muscle of foot.
O.F.R. = Optic fibre layer of retina.
O.G. = Olfactory or pedunculate ganglion.
O.I.G. = Opening of ink gland.
O.L. = Outer circular lip.
O.M.A. = Oblique muscle zone of arm.
O.M.B. = Oblique retractor muscle of buccal mass.
O.N. = Olfactory nerve.
O.OD. = Opening into mantle cavity of oviduct.
O.P. = Olfactory pit.
OP.G. = Optic ganglion.
OP.N. = Optic nerve.
O.P.S. = Opening of duct of posterior salivary glands at end of tongue.
OR. = Orbit of eye.
O.S. = Optic sinus.
O.S.V. = Opening from peri-oesophageal sinus into sinus vein.
O.T. = Orifice of testis opening into viscero-pericardial coelom.
O.V. = Ophthalmic vein.
O.V.C. = Opening of vena cava into branchial heart.
O.VP. = Outline of viscero-pericardial coelom.

P. = Pedal ganglion.
PA. = Pancreatic appendages of duct of digestive gland.
P.A.F. = Posterior adductor muscle of funnel.
P.AO. = Posterior aorta.
P.A.V. = Posterior azygos vein.
P.B. = Posterior ctenidia or branchia.
P.B.H. = Position of branchial heart in viscero-pericardial coelom.
P.B.S. = Peri-buccal blood sinus.
P.C.N. = Posterior nerve of cephalic vein.
P.D.C. = Proximal deferent canal.
P.F. = Posterior end of fin.
P.F.A. = Posterior fin artery.
P.FI.V. = Posterior fin vein.
P.F.M. = Posterior conjunctive fin muscle.
P.F.N. = Posterior funnel nerve.
P.FU.A. = Posterior funnel artery.
P.F.V. = Posterior funnel vein.
P.G.A. = Posterior accessory genital artery.
P.GL. = Pericardial gland.
P.G.V. = Posterior accessory genital vein.
P.H.R.N. = Posterior nerve of retractor muscle of head.
P.I.G. = Pigment-secreting part of ink gland.

PL. = Pleural ganglion.
P.L. = Palatine lobe containing anterior salivary gland.
P.L.R. = Pigmented layer of retina.
P.M. = Posterior chamber of mantle cavity.
P.M.A. = Posterior mantle artery.
P.M.C. = Posterior elastic boundary of mantle cavity.
P.M.V. = Posterior mantle vein.
P.N. = Pallial nerve.
P.O.A. = Posterior oesophageal artery.
P.O.M.N. = Posterior oculomotor nerve.
P.O.N. = Postorbital nerve.
P.O.S. = Peri-oesophageal blood sinus.
PR. = Proostracum.
P.R.A. = Posterior renal artery.
PR.M. = Primitive mantle.
P.RO. = Position of rostrum of shell.
P.S. = Protuberances of statocyst.
P.S.G. = Posterior salivary or poison gland.
P.SH. = Posterior part of shell margin.
P.S.I. = Posterior sphincter muscle of inksac.
P.S.V. = Posterior shell sac vein.
P.T.P. = Position of tentacle pocket.
P.V.C. = Posterior visceral commissure.
PV.G. = Pleurovisceral ganglion.
PV.N. = Pleurovisceral nerve.
P.VP.C. = Posterior limit of viscero-pericardial coelom.
P.V.R.M. = Posterior vein to retractor muscles of head and funnel.
P.Z. = Pigment zone of retina.

R. = Rods of retina.
RA. = Radula.
R.A. = Rectal artery.
R.C. = Radula cartilage.
R.D.C. = Ridge on dorsal cartilage.
RE. = Rectum.
RE.A. = Renal appendages of veins.
RE.N. = Retinal nerves.
RE.P. = Renal papilla.
RE.S. = Renal sac.
R.F. = Retractor muscle of foot.
R.F.A. = Artery to retractor muscle of funnel.
R.F.B. = Respiratory filament of branchia.
R.F.C. = Retractor muscle of fin cartilage.
R.FU. = Retractor muscle of funnel
R.G. = Radula gland.
R.H. = Retractor muscle of head.
R.H.A. = Artery to retractor muscle of head.
R.I. = Reservoir of inksac.
R.IN. = Grooved longitudinal ridge of intestine.
R.M. = Radula membrane which slides over odontophore.
R.M.A. = Radial muscle zone of arm.
R.M.T. = Radial muscle zone of tentacle.
R.M.V. = Right genito-mesenteric vein.
R.N. = Renal nerves.
RO. = Rostrum.
R.R. = Retractor muscle of radula
R.V.H. = Ring vein of head.

S. = Blood sinus.
S.A. = Siphuncle artery.
S.A.N. = Superior antorbital nerves.
S.A.O.N. = Superior anterior ophthalmic nerve.
SA.S. = Sac of Spermatophore.
S.B.G. = Superior buccal ganglion.
SC. = Statocyst.
S.C. = Sphincter muscle of caecum.
SC.C. = Statocyst cartilage of skull
SC.CA. = Sclerotic cartilage of eyeball.
S.CE. = Sensory cell of retina.
S.D.P. = Septum of dorsal part of phragmocone.
S.G. = Stellate ganglion.
SH. = Shell.
S.H. = Systemic heart.
SH.E. = Shell epithelium.
SI. = Siphuncle.
S.I. = Sphincter muscle of intestine.
SI.V. = Vein from head sinuses to cephalic vein.
SK. = Skin.
S.M. = Swimming margin of tentacle head.
S.M.C. = Median septum of mantle cavity.
S.N. = Sympathetic nerve (paired).
S.O. = Sphincter muscle of oesophagus.
S.P.I. = Scleral plate of iris.
S.P.O.N. = Superior posterior ophthalmic nerve.
SP.R. = Sperm reservoir of spermatophore.
S.R. = Siphonal region of dorsal part of phragmocone.
S.RE. = Sphincter muscle of rectum.

S.S. = Sphincter muscle of stomach.
S.SU. = Stalk of sucker.
ST. = Stomach.
ST.N. = Nerves of stomach.
S.T.S. = Striations of trabeculae of shell.
SU. = Sucker.
SU.C. = Chamber of sucker.
SU.P. = Sucking pad.
S.V. = Siphuncle vein.
S.VE. I. = Seminal vesicle I.
S.VE. III. = Seminal vesicle III.

T. = Tongue.
T.A. = Tentacle artery.
T.B. = Tie-bar in muscular chamber of cephalic vein.
TE. = Testis.
TEN. = Tentacle
T.F. = Terminal filament of spermatophore.
T.M.F. = Transverse muscle of funnel.
T.N. = Tentacle nerve.
T.P. = Terminal pad of tentacle head.
T.PO. = Tentacle pocket.
T.P.V. = Vein from ventral part of tentacle pocket.
TR. = Trochlear cartilage of skull.
T.S. = Tunic of spermatophore.
T.V. = Tentacle vein.
T.VP. = Transverse flap of viscero-pericardial coelom.
TW.S. = Twist of spermatophore.

V. = Vestibule between stomach, caecum and intestine.
V.A.A.V. = Valve of anterior azygos vein.
V.A.V. = Paired valves guarding opening from auricle into ventricle.
V.B.G. = Vein of branchial gland.
V.B.M. = Vein of branchial muscle.
V.C. = Vena cava.
V.C.A. = Valve guarding opening from ventricle into cephalic artery.
V.CH. = Ventral chamber of renal sac.
VE. = Ventricle.
V.F. = Ventral surface of fin.
V.F.ME. = Ventro-lateral fin membrane.
V.G. = Visceral ganglion.
V.G.A. = Ventral gastric artery.
V.H.V. = Ventral head vein.
V.J. = Ventral jaw.
V.N. = Visceral nerve.
V.N.G. = Vein of nidamental gland.
V.O.A. = Ventral orbital artery.
VP. = Viscero-pericardial coelom
V.P.A. = Valve guarding opening from ventricle into posterior aorta.
V.P.A.V. = Valve of posterior azygos vein.
V.PH. = Ventral part of phragmocone, which grows back.
V.R.S. = Vein from ring vein to peri-buccal sinus.
V.S.A. = Median shell sac artery.
V.T. = Ventral sucker margin of tentacle.

W.B. = White body.
W.G.S. = Wall of genital sac.
W.O. = Wing of orbital cartilage of skull.

Y.CH. = Yellow chromatophore.

DESCRIPTION OF PLATES

(All except Figures 1 and 2 were drawn from preserved material.)

PLATE I.

Fig. 1. *Sepia officinalis* swimming. The figure was drawn from sketches taken of specimens at Brighton aquarium. The animal is gently propelling itself forwards by undulating waves which travel along the fins. The arms are in their normal position, with the tips close together. × ½.

Fig. 2. In pursuit of a shrimp. The tentacles are in the act of being shot out from the tentacle pockets in which they normally lie. They come out together working like a pair of tongs. At the same time the arms are extended, and opening to envelop the prey. × ½.

Fig. 3. Male specimen: ventral view. × ⅓.

Fig. 4. Male specimen: dorsal view. × ⅓.

PLATE II.

Fig. 5. Mantle cavity of male specimen. The mantle cavity has been exposed by a median longitudinal cut through the mantle wall. The median mantle artery and vein (M.A.V.), which travel along the edge of the septum dividing the posterior part of the mantle cavity into two, have been severed. The renal appendages and branchial hearts are showing through the semi-transparent wall of the visceral dome. The tentacles are withdrawn within the tentacle pockets and so are not visible. × ⅔.

Plate III.

Fig. 6. Mantle cavity of female specimen. The mantle cavity and funnel have been opened by median longitudinal cuts. The septum dividing the posterior part of the mantle cavity into two has been removed, exposing the vestigial siphuncle artery and vein (S.A. and S.V.). The ovary shows through the semi-transparent posterior part of the visceral dome. The very large nidamental and accessory nidamental glands (N. and AC.N.G.) are attached to the posterior part of the visceral dome. *Only the parts not displayed, or not lettered in Figure 5, are lettered in this figure.* × ⅔.

Plate IV.

Fig. 7. Anterior view of the mouth and arms of a female specimen. × ½.

Fig. 8. Section through the skin, taken from the back of *Sepia officinalis*, to show the position of the chromatophores and iridocytes. (After Kühn and Heberdey, from unstained preparations). Highly magnified.

Fig. 9. Surface view of the skin from the back of *Sepia officinalis*. On the left side the chromatophores are in focus; on the right, the deeper lying iridocytes. In surface view the iridocytes have optically empty centres. (After Kühn and Heberdey, from unstained preparations). Highly magnified.

Fig. 10. Diagram of a single chromatophore. (*a*) Contracted. (*b*) Expanded. The muscle fibres should be about four times as long as they are actually drawn. (Adapted from Bozler). Highly magnified.

Fig. 11. Right tentacle. × 1.

Fig. 12. Hectocotylised arm of male. × ½.

Fig. 13. Optical section through a typical sucker taken from arm number 3. × 15.

Fig. 14. Surface view of the mouth of a typical sucker. × 15.

Plate V.

Fig. 15. The shell of a male specimen : ventral view. × ⅔.

Fig. 16. Median optical section through the shell. × ⅔.

Fig. 17. Median section through the posterior part of the shell, to show how the ventral part of the phragmocone grows back posteriorly. × 5.

Fig. 18. Some of the septa of the dorsal part of the phragmocone, to show the transverse striations on the trabeculae. × 10.

Fig. 19. Part of a shell in which part of the dorsal surface has been broken away to show the form of the trabeculae, which form a maze-like framework supporting the septa of the dorsal part of the phragmocone. × 1½.

Plate VI.

Fig. 20. Dissection of the coelomic cavities of a male specimen. The thick lines represent the outlines of the various chambers of the body cavity. The inksac has been dissected away from the ventral wall of the viscero-pericardial coelom, leaving the posterior mantle artery (P.M.A.) which runs ventral to it intact. The ventral renal chamber (V.CH.) has been opened by slitting the renal papillae (RE.P.), and the entire ventral wall of this cavity has been removed. Part of the rectum (RE.) has been cut away to expose the fork of the cephalic vein (CE.V.) into the two venae cavae (V.C.).

The renal appendages (RE.A.) have all been clipped off on the left side, to show the course of the veins. The coelomic spaces around the branchial hearts (B.H.) have been opened, and the branchial heart on the left side is shown in section to illustrate the course of the blood to the branchia. The afferent (A.V.) and efferent (E.V.) vessels of the left branchia have been dissected out, and the factors contributing to the left anterior mantle vein (A.M.V.) have been exposed. A window has been cut in the posterior, or visceral part of the viscero-pericardial coelom, through which part of the testis (TE.) and stomach (ST.) can be seen. The outline of the anterior part of the viscero-pericardial coelom (O.VP.) is shown by broken lines. It communicates on either side with the ventral renal chamber by small apertures (A.VP.C.) at the bases of the renal papillae. A small window has been cut through the wall of the posterior part of the dorsal renal chamber (C.D.C.), exposing part of the spiral caecum (CA.). The outline of the rest of this cavity which opens into the ventral renal chambers anteriorly by a large orifice (L.V.D.) is shown by broken lines (O.D.C.). The outline of the ink gland (I.G.) showing through the dorsal surface of the inksac is shaded. The position of the clear central portion of this gland (C.I.G.) is also shown. × $\frac{3}{4}$.

PLATE VII.

Fig. 21. The viscero-pericardial coelom, and the dorsal chamber of the renal sac of a male specimen. This figure is rather diagrammatic. Thick lines represent the cut edges of the walls of the body cavities, which have been removed to expose the organs lying within them.

All but the most anterior part of the ventral renal chambers (V.CH.) together with the branchial hearts and veins associated with them have been removed, but the communication (C.V.C.) just posterior to the ventricle (VE.) in the middle line between the right and left ventral chambers, is shown. The loop of the intestine (IN.) and part of the rectum (RE.) have been removed. All the ventral wall of the viscero-pericardial coelom (VP.) except the pouch (P.B.H.) of the right branchial heart, the transverse flap (T.VP.) which forms the dorsal wall of this pouch, and the anterior funnel-shaped parts leading to the apertures (A.VP.C.) of the coelom into the renal sac have been cut away, together with the male genital duct. In addition part of the dorsal wall which separates the viscero-pericardial coelom from the dorsal chamber (D.C.) of the renal sac has been removed. The ventricle of the arterial heart has been cut through, and the left-hand part which receives the left auricle has been removed. The ducts of the digestive glands (D.L.) are represented as having had most of their appendages (PA.) clipped off, and holes show where the cavities of these appendages opened into them. $\times \frac{3}{4}$.

Fig. 22. Diagram of the viscero-pericardial coelom and the renal sac of a male specimen. In this diagram the ventral wall of the ventral chambers of the renal sac are represented as having been cut away. The thick line (C.V.R.) represents the cut edge. The outline of the transverse flap (T.VP.) of the viscero-pericardial coelom (VP.) and most of the dorsal renal chamber (D.C.) are shown by broken lines as they are obscured by other parts of the body cavities. $\times \frac{3}{4}$.

Plate VIII.

Fig. 23. Dissection of the muscles of the funnel. The funnel has been opened by a longitudinal cut a little to the left of the middle line. Some of the skin of the ventral side of the head has been dissected away and part of the dorsal wall of the funnel has been freed from the head so that it could be turned back. The various muscles have been freed from the connective tissue which somewhat obscures them, and part of the cephalic vein (M.CE.V.) has been cut away, to show the diaphragm cartilage (D.CA.) lying immediately dorsal to it. × ⅔.

Fig. 24. Transverse section through the neck and mantle to show the relations of the muscles. × ⅔.

Plate IX.

Fig. 25. Ventral dissection of the muscular system. The mantle (M.M.) has been opened by a median longitudinal incision. The funnel has been cut through longitudinally along the middle line, the right half being freed from the head and neck, to which it is attached by the adductor muscles, and it has been displaced to the side. The adductor muscles of the funnel have been completely removed. The left retractor muscle of the head has been dissected away from the cephalic and brachial cartilages, and the left half of the funnel together with the left retractor muscles of the head and funnel have been almost completely cut away, so that only the more dorsally situated parts of these muscles remain. The anterior cephalic vein (Fig. 23, A.C.V.) has been removed. The diaphragm cartilage has been removed and a cut edge (A.D.C.) shows where the retractor muscle of the head was attached to it. The viscera

constituting the visceral dome have been removed *en masse*, leaving only the posterior salivary glands (P.S.G.) and the anterior part of the oesophagus (OES.) and cephalic artery (CE.A.) *in situ*. The shell epithelium on the ventral side of the shell has been cut away, so that the shell (SH.) can be seen bordered by the muscles. The pallial nerves (P.N.) and the anterior part of the visceral nerves (V.N.) have been left intact, but both the anterior and the posterior funnel nerves have been removed. The position of their emergence from the skull is indicated by the foramina (F.A.F. and F.P.F.). On the right side of the head a window has been cut to show the position of the pocket (T.PO.) in which the tentacle is kept, while on the left the ventral wall of this pocket has been completely removed so that the origin of the tentacle (TEN.) and its attachment to the brachial cartilage (BR.C.) can be seen. On the left side part of the eye has also been exposed. Part of the left branchia has also been dissected away to show the course of the retractor muscle of the branchia (A.R.B. and M.R.B.). × ½.

Fig. 26. Cephalic cartilage: posterior view. *The ventral side is uppermost.* The membrane (M.P.B.) enclosing the posterior part of the brain has been left intact, and the paired buccal arteries (B.A.), the oesophagus (OES.) and the duct (D.S.G.) of the posterior salivary glands, all of which lie freely in the peri-oesophageal blood sinus (P.O.S.) are shown in transverse section. × ⅔.

Fig. 27. Cephalic and brachial cartilages: ventral view. The brachial cartilage (BR.C.) is drawn in the position it occupies relative to the cephalic cartilage. × ⅔.

Fig. 28. View of the right orbit of the cephalic cartilage, to show the foramina and nerves. *The ventral side is uppermost.* × $\frac{2}{3}$.

Fig. 29. Anterior view of the cephalic and brachial cartilages. *The ventral side is uppermost.* The brachial cartilage (BR.C.) has been displaced away from the cephalic cartilage, which it would partly obscure if it were left in its natural position relative to the former. × $\frac{2}{3}$.

PLATE X.

Fig. 30. Posterior view of a transverse section of the left fin, taken at about the middle of the fin. This figure shows only the swimming muscle of the fin, and the fin cartilage. The skin covering the swimming muscle, and the muscles and membranes attached to the fin cartilage have been removed. The cut surface of the swimming muscle shows muscle fibres running in three directions, longitudinally, laterally and dorso-ventrally. The details of the muscle fibres were taken from transverse sections of a very young specimen viewed under the microscope. × $1\frac{1}{2}$.

Fig. 31. Mesial view of the left fin cartilage (FI.C.), together with the muscles and membranes attached to it. × $\frac{1}{2}$.

Fig. 32. Dorsal dissection of the back to show the relations of the fin (FI.) to the shell (SH.) and mantle (M.M.), and also to show the dorso-lateral and posterior conjunctive fin muscles. (D.F.M. and P.F.M.). × $\frac{1}{2}$.

Fig. 33. Ventral view of the diaphragm cartilage (D.CA.) to show its foramina, and the muscles attached to it. It has been exposed by removing the funnel, and dissecting away the cephalic vein, which is attached to it. × $\frac{2}{3}$

Fig. 34. Dorsal view of the nuchal cartilage. The origin of the inner and outer collar muscles (I.C.F. and O.C.F.) of the funnel have been left attached on one side. × ½.

Fig. 35. Ventral view of the dorsal cartilage. The muscular mantle and the retractor muscles of the head and funnel, which have their origin on the posterior part of this cartilage, have been dissected away. Posteriorly this cartilage is very thin, and indefinite in outline, consisting of a tough membrane, reinforced by a little cartilage. × ½.

PLATE XI.

Fig. 36. Ventral view of the digestive system, showing also the retractor muscles (O.M.B. and L.M.B.) of the buccal mass, and the blood sinuses of the head. The peri-buccal sinus (P.B.S.) has been exposed by cutting through the middle of arms number 3 on both sides in the longitudinal plane. The ventral half of the head has been removed, together with the left half of the cephalic cartilage (C.C.). Posterior to the skull the digestive system has been completely isolated from the body, and the ducts (D.L.) of the digestive glands (L.) have been dissected away from the oesophagus and intestine, to which they were attached. Part of the pancreas (PA.) has been clipped off the right duct. × 1.

PLATE XII.

Fig. 37. Dorsal dissection of the buccal mass. The buccal mass has been exposed by opening the peri-buccal sinus (P.B.S.) along the mid-dorsal line. The dorsal half of the jaw muscles and of the retractor muscles of the buccal mass have been cut away. The dorsal jaw has been

removed, and it is shown in Figure 38 displaced to one side, but otherwise as it would appear *in situ*, covering the palatine lobes (P.L.). The left wing of the ventral jaw (V.J.) has been cut away. The right palatine lobe has been pulled to one side to show the opening (O.A.S.) of the anterior salivary gland. The anterior part of the horny lining (H.OES.) of the oesophagus, which extends forwards between the palatine lobes to their anterior extremity has been removed. The peri-oesophageal sinus is represented as being cut through posteriorly, to show the buccal arteries (B.A.), oesophagus (OES.), and duct (D.S.G.) of the posterior salivary glands, which lie in it. *The whole buccal mass has been pulled forward, so that the figure might be clearer.* In consequence the blood sinuses appear to be larger than is actually the case in an undissected specimen. × 1½.

Fig. 38. Dorsal view of the dorsal jaw. The horny lining of the oesophagus (H.OES.) which is attached to the posterior end of the jaw has been left adhering. The dorsal part of this jaw forms the dorsal wall of the groove between the palatine lobes which leads to the oesophagus. × 1½.

Fig. 39. The anterior part of the radula: postero-lateral view. This is a diagrammatic figure to show the way in which the radula membrane (Fig. 40, R.M.), bearing the horny radula, fits over the odontophore (OD.), which is U-shaped in cross section. For the explanation of the cut surface see Figure 40, which shows this surface in full view. × 3.

Fig. 40. Transverse section through the anterior part of the radula. This figure, which was drawn from a hand section, shows the odontophore (OD.) supported by paired cartilaginous rods (R.C.). The teeth shown are young ones

which are not sufficiently anterior to be yet in use. Muscles (R.R. and A.R.) which pull the radula to and fro over the odontophore are shown. They lie in the radula membrane (R.M.). × 4.

Fig. 41. Transverse section through the radula, rather more posterior than Figure 40 : drawn from a hand section. This figure shows the radula gland (R.G.) which secretes the radula teeth, and the horny cuticle from which the teeth project. Part of the left palatine lobe (P.L.) is shown. This contains the anterior salivary gland (A.S.G.). The right palatine lobe has been cut away at the base. Cut ends (M.J.) show where the radula-tongue assemblage was attached to the jaw muscles which form the outer part of the buccal mass. × 4.

Fig. 42. Three rows of radula teeth. (After Naef.). × 8.

Fig. 43. Longitudinal section through the inksac, and the anterior part of the rectum, to show the general structure. In the ink gland two zones can be recognised, a clear central one (C.I.G.), and an outer zone (P.I.G.) in which the cells are forming pigment. × 1.

Fig. 44. The jaws : lateral view. The dorsal jaw has been displaced dorsally from the position it occupies relative to the ventral jaw, as otherwise the latter would partially obscure it. × 1.

Fig. 45. Part of a single lamina from the wall of the spiral caecum, to show the ribbed structure, which increases its surface. × 8.

Fig. 46. Stomach and caecum opened, to show the gross structure. The figure is somewhat diagrammatic. Most of the ventral wall of the stomach (ST.), the vestibule (V.) and the caecum (CA.) have been removed, but the ventral part of the groove (G.C.S.) along which the secretion of the digestive glands is conducted to the stomach, has only been cut

through, and the walls pulled apart. The stomach is completely lined with horny material (H.S.). This lining, however, is very thin except in the region of the circular grinding muscle (C.M.S.). Three sphincter muscles (S.S., S.C. and S.I.) are shown in the vestibule, a region with which the stomach, caecum and intestine all communicate. These muscles control the direction of flow of the contents. The surface of the caecum is greatly increased by numerous laminae (L.CA. and Fig. 45) which lie radially, though only some of them stretch right from the columella to the periphery. × ⅔.

PLATE XIII.

Fig. 47. Diagram of the arterial system: ventral view. The brain (V.G., P. and BR.G.) right optic ganglion (OP.G.) have been drawn in place so that the course of the arteries through the ganglia could be shown. The right pallial nerve (P.N.) the posterior salivary glands (P.S.G.), the stomach (ST.), caecum (CA.) and testis (TE.) have also been drawn to act as landmarks. × ⅔.

PLATE XIV.

Fig. 48. Diagram of the venous system: ventral view. The segments of the arms and tentacles, included in the figure to show the origin of the various veins from the arms and tentacles, have been drawn smaller than their true proportions relative to the rest of the figure. This was done for the sake of clearness. × ⅔.

PLATE XV.

Fig. 49. Optical section through the anterior half of the animal, drawn from a lateral dissection. Although the left half has been cut away,

some of the vessels and nerves on this side have been left in place. Neither the cartilage of the skull, nor the ganglia of the brain are lettered, but the former is indicated by black dots, and the latter are drawn black, and can be identified by comparison with Figure 79. The course of the arteries in the head will become clearer if this figure is compared with Figure 47. *The animal is represented as lying on its back, as this is the position it usually occupies during dissection.* × 1¼.

Plate XVI.

Fig. 50. Transverse section through arm Number 3, to show the muscle zones. × 3.

Fig. 51. Transverse section through one of the tentacles to show the muscle zones. × 4.

Fig. 52. The systemic heart : ventral view. The ventral wall of the ventricle (VE.) has been removed so that the valves guarding the entry of the auricles (AU.) and the exits of the cephalic artery (CE.A.) and posterior aorta (P.AO.) can be seen. × 1.

Fig. 53. A small portion of one of the branchiae showing the primary and secondary folding of the respiratory filament of one of the laminae. × 5.

Fig. 54. Mesial view of the right branchial heart, and part of the branchia, to illustrate the general anatomy and the branchial circulation. The figure is somewhat diagrammatic. × 2.

Plate XVII.

Fig. 55. Dorsal view of the nervous system. The right stellate ganglion and the nerves of the right fin have been omitted for the sake of clearness. The sympathetic system has been drawn black. (Slightly modified from Hillig.) × ⅔.

Plate XVIII.

Fig. 56. Lateral view of the brain and nerves which leave it, from the right side. The optic nerve (C.O.N.) is represented as having been cut through close to the brain, and the brachial and tentacle nerves of the left side have been omitted. (Considerably modified from Hillig.) × 3.

Plate XIX.

Fig. 57. Dorsal view of the central nervous system and the nerves which emerge from it. The left optic ganglion (OP.G.) has been included. A portion of the oesophagus (OES.) has been left in place to show where it passes through the brain. × 2½.

Fig. 58. Dorsal view of the central nervous system, to show the grooves (G.P.B. and G.V.P.) separating the visceral, pedal and brachial ganglia, and also the relations of the branches of the cephalic artery (CE.A.) to the brain. The right half of the cerebral ganglion has been removed, and the membrane lining the peri-oesophageal blood sinus, which passes through the brain, has been stripped away. The left optic ganglion (C.O.G.) is shown in section. × 2½.

Plate XX.

Fig. 59. Dorsal view of the left eye *in situ*, after the orbit has been opened, and the dorsal wall bent to the side. The optic sinus has been opened by cutting a window through the membrane (E.A.) which attaches the eye to the skull. Part of the white body (W.B.) can be seen lying in the sinus. × ½.

Fig. 60. Mesial view of the left eyeball as seen from a slightly dorsal aspect. The membrane (E.A.) holding the eye to the cartilaginous part of the

orbit has been cut away close to the eye. All the extrinsic muscles of the eye which are attached to this membrane were cut away at the same time, except for the trochlear muscle III (M.TR., III.) which is inserted on the inner ventral surface of the sclerotic cartilage (SC.CA.). The end of the ophthalmic artery (O.A.) has been left in place. The retinal nerves have been cut through close to the sclera through which they pass by means of numerous foramina (F.R.N.). × 1½.

Fig. 61. Dorsal view of the eyeball attached to the skull, to show the superior oculomotor muscles. × 1.

Fig. 62. Posterior view of the eyeball attached to the skull, to show the posterior oculomotor muscles. × 1.

Fig. 63. Ventral view of the eyeball attached to the skull, to show the inferior oculomotor muscles. × 1.

Fig. 64. Mesial anterior view of the eyeball attached to the skull, to show the conjunctive and trochlear oculomotor muscles. × 1.

Fig. 65. Mesial anterior view of the eyeball attached to the skull. The trochlear cartilage has been cut off, and the conjunctive oculomotor muscles, and the trochlear oculomotor muscles I and II removed, to show the anterior oculomotor muscle I (M.A., I.) and the trochlear oculomotor muscle III (M.TR., III). × 1.

PLATE XXI.

Fig. 66. Ventral view of the left eyeball, dissected to show its structure. × 2½.

Fig. 67. Dorsal view of a section through the left eye and orbit. The section is through the anterior-posterior plane of symmetry of the

eyeball, and therefore slopes a little towards the dorsal side as it passes from the centre of the animal. × 2.

PLATE XXII.

Fig. 68. Diagrammatic posterior view of the anterior part of the statocysts, which have been cut in half in the transverse dorso-ventral plane: to show the position of the macula and the crista, which cannot, however, be seen by macroscopic methods of investigation. (From Hamlyn-Harris.) × 6.

Fig. 69. Diagrammatic anterior view of the posterior part of the statocysts, which have been cut in half in the transverse dorso-ventral plane: to show the crista and protuberances (P.S.). The cut surfaces in this figure and Figure 68 fit against one another. (From Hamlyn-Harris.) × 6.

Fig. 70. Statolith from the right statocyst: (*a*) dorsal view, (*b*) ventral view. × 8.

Fig. 71. Diagram of the structure of the cephalopod retina. Three sensory cells (S.CE.) are shown, between which lie four limiting cells (L.C.). The sensory cells bear the rods (R.) between which go secretion threads (C.L.M.) from the limiting cells to the limiting membrane (L.M.) Each rod and sensory cell is linked by a meandering neurofibril (NF.) which forms a little knob at the inside end, while on the outside it enters the sensory nerve (N.O.G.) to the optic ganglion. Outside the limiting cells lies the basal membrane (B.ME.), secreted by connective tissue cells (C.CE.). The three rods show the pigment in different positions. On the left the adjustment is for bright light, and on the right it is for seeing in very poor light. The middle rod shows an intermediate stage. (Figure from Hesse, partly after Lenhossék.)

Fig. 72. Ovary and oviduct of an immature female. The ventral wall of the viscero-pericardial coelom (C.VP.) has been cut away on the left side close to where it attaches to the wall of the dorsal chamber (D.C.) of the renal sac. The oviduct has been freed from the structures which cover it on the ventral side. The figure is of an immature specimen since at maturity the whole posterior part of the coelom is distended with eggs. × 1.

Fig. 73. A cluster of eggs of *Sepia officinalis*. (After Jatta.) × ½.

Plate XXIII.

Fig. 74. Ventral view of the male genital duct, which has been dissected away from the body. The genital sac (G.S.) has been cut open. × 1.

Fig. 75. Dorsal view of the male genital duct, the component parts of which have been separated. × 1.

Fig. 76. Dorsal view of an optical section through the accessory gland (A.G.), the appendage (A.A.G.) of the accessory gland, and adjacent parts. (Modified from Blanquaert.) × 2½.

Fig. 77. A single spermatophore. (After Blanquaert.) × 50.

Fig. 78. The explosion apparatus of a single spermatophore. (After Blanquaert.) × 100.

Plate XXIV.

Fig. 79. Diagrammatic longitudinal optical section through *Sepia*: to show the general body organisation. × ½.

Fig. 80. Diagrammatic transverse section through the head. The section has passed through the extreme anterior part of the orbit (OR.). × ¾.

Fig. 81. Diagrammatic transverse section through the body, a little posterior to the anus: viewed posteriorly. × ¾.

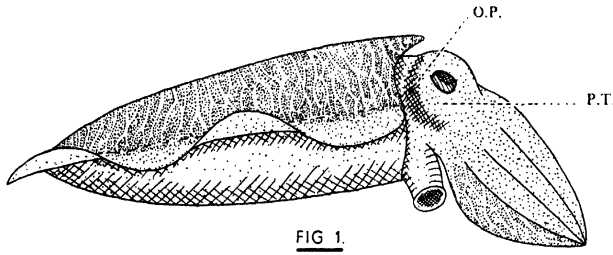

FIG 1.

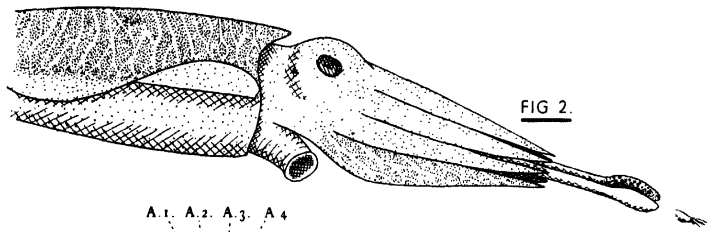

FIG 2.

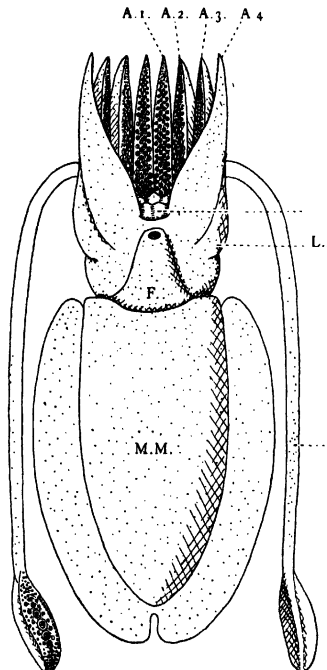

FIG. 3.

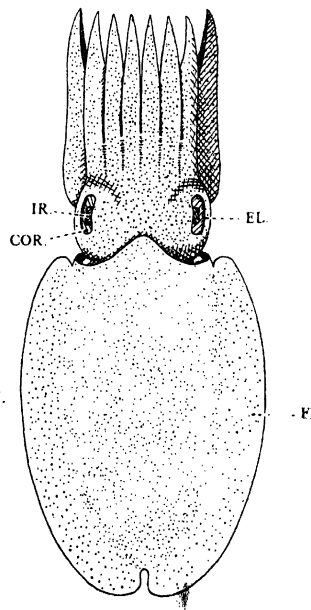

FIG. 4.

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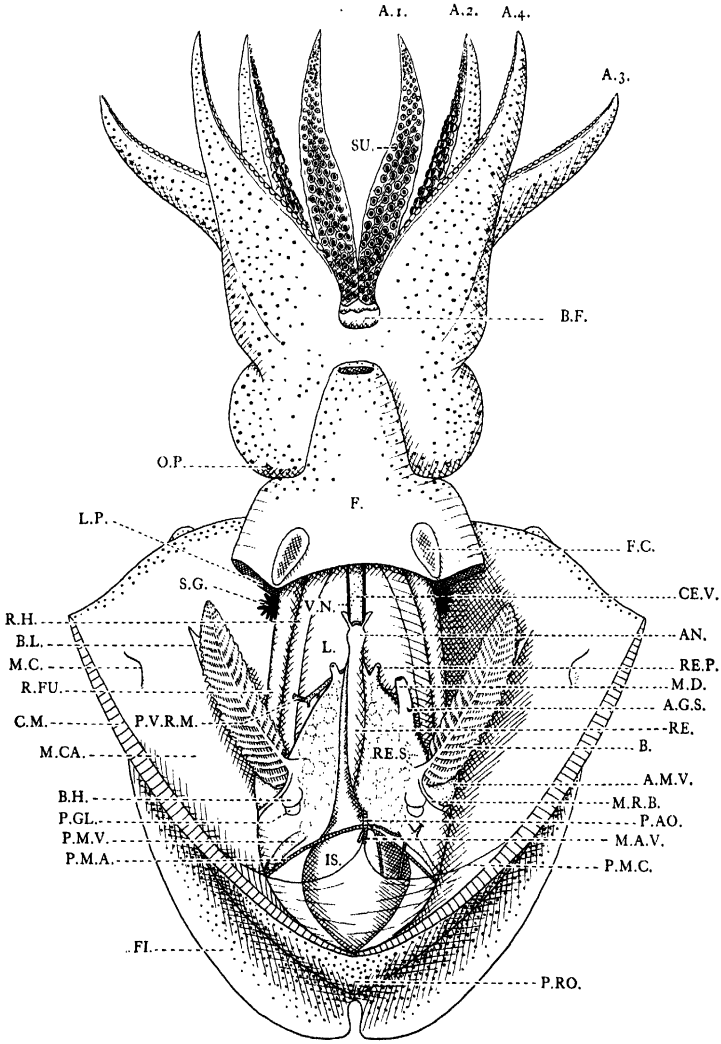

FIG. 5.

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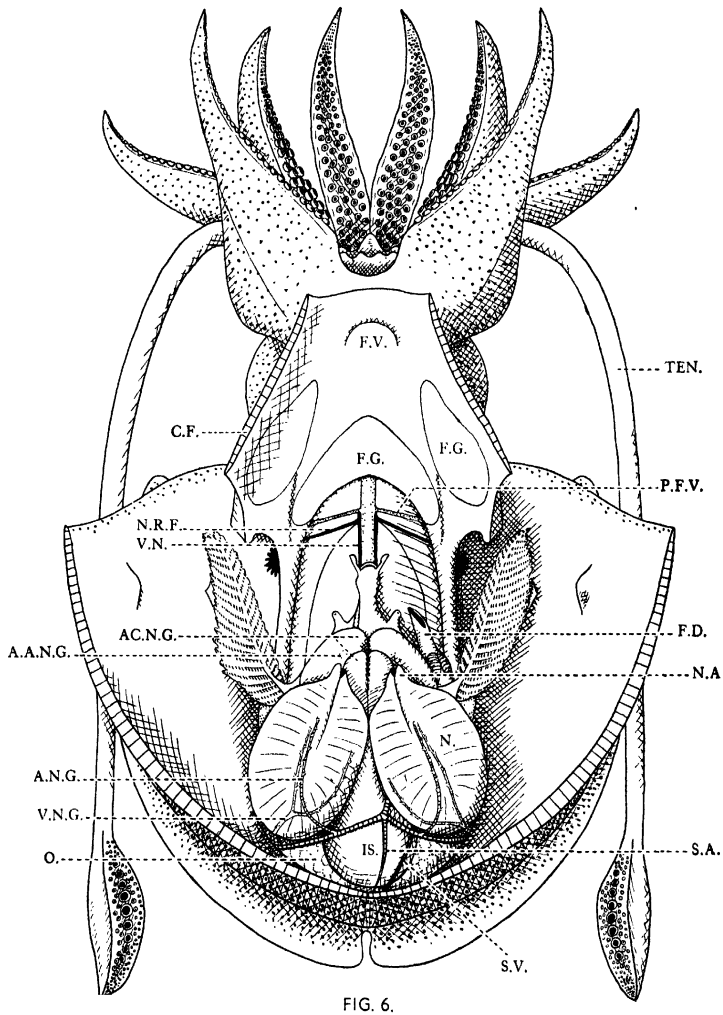

FIG. 6.

For lettering of other parts, see Plate II.

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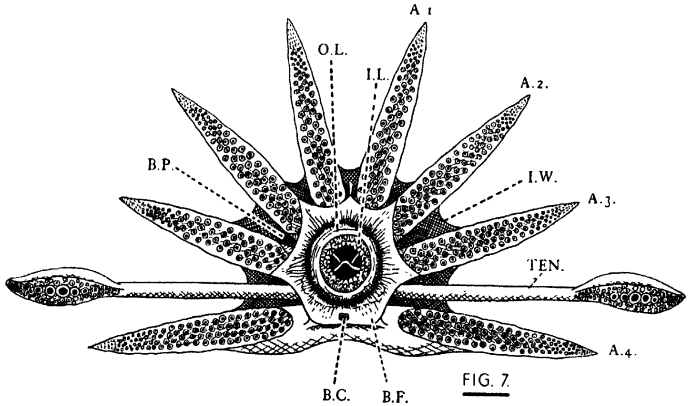

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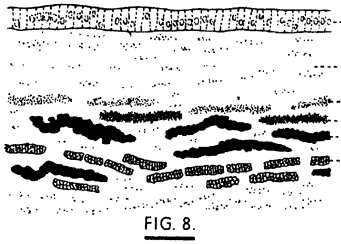

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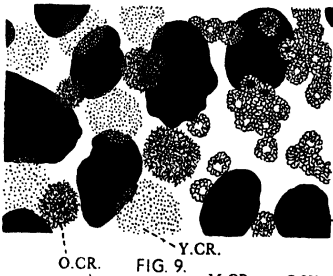

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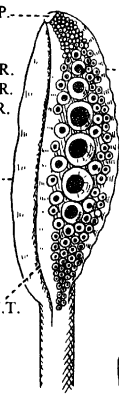

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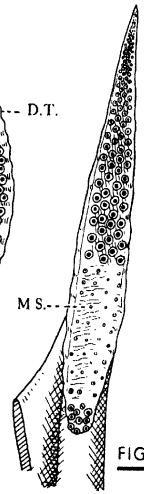

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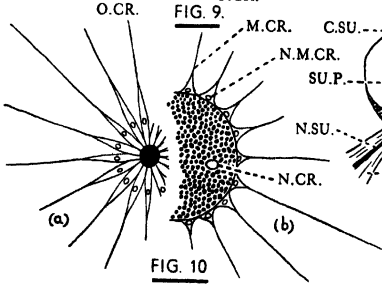
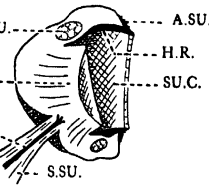


FIG. 10



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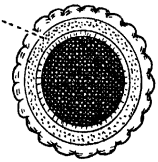

FIG. 14.

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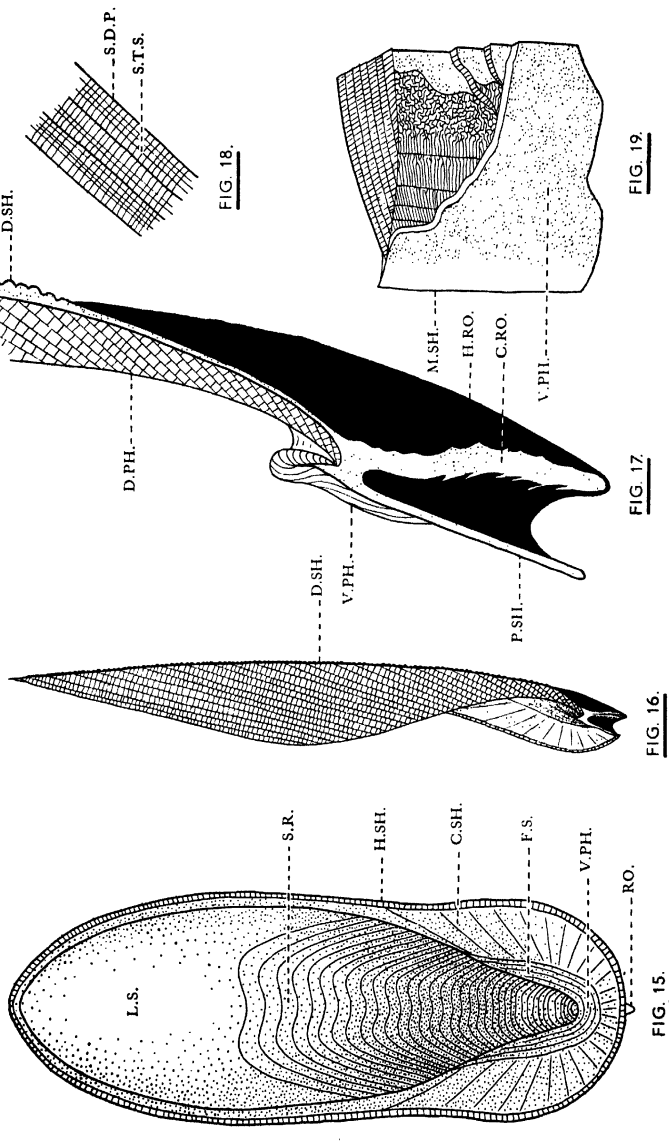

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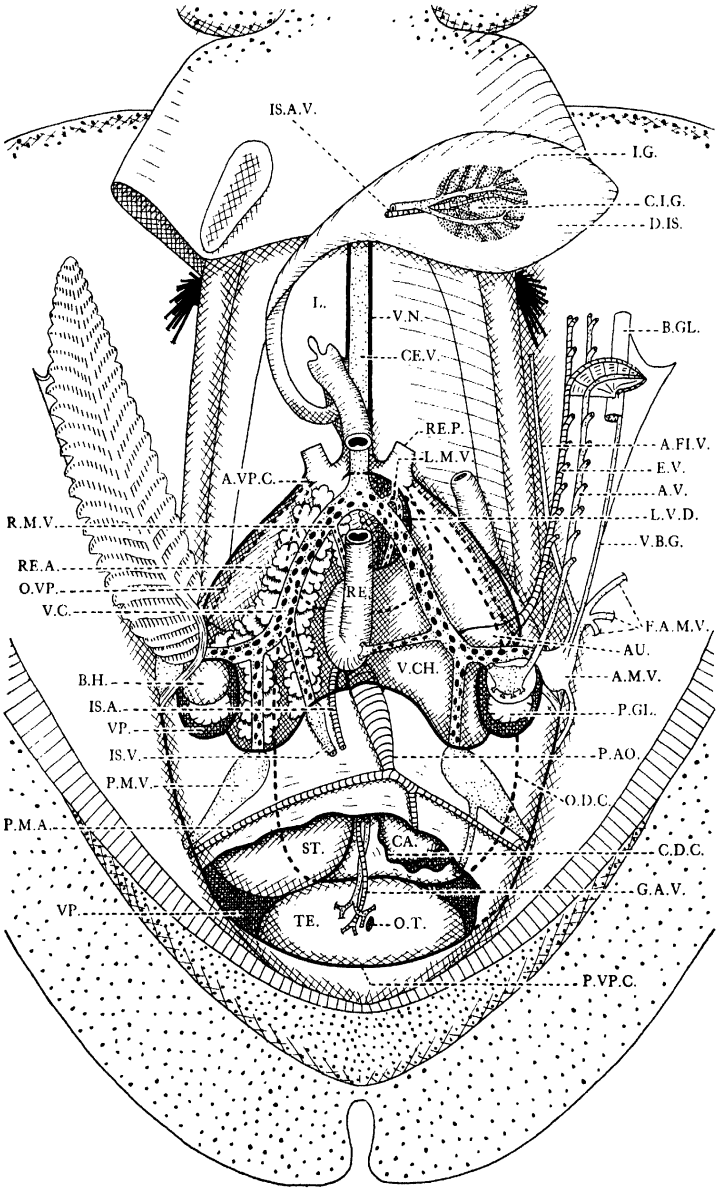

FIG. 20.

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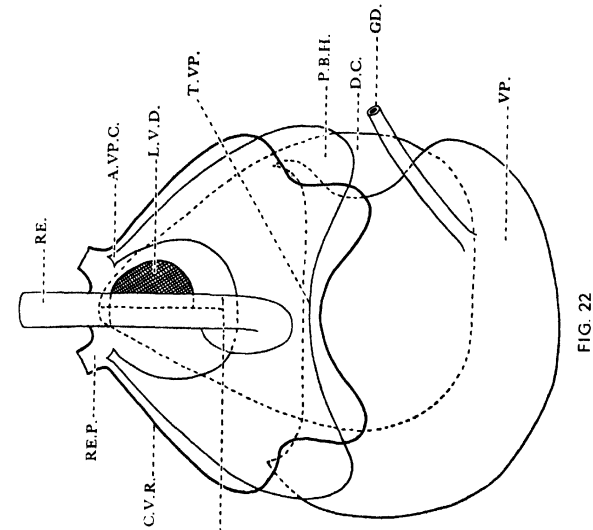

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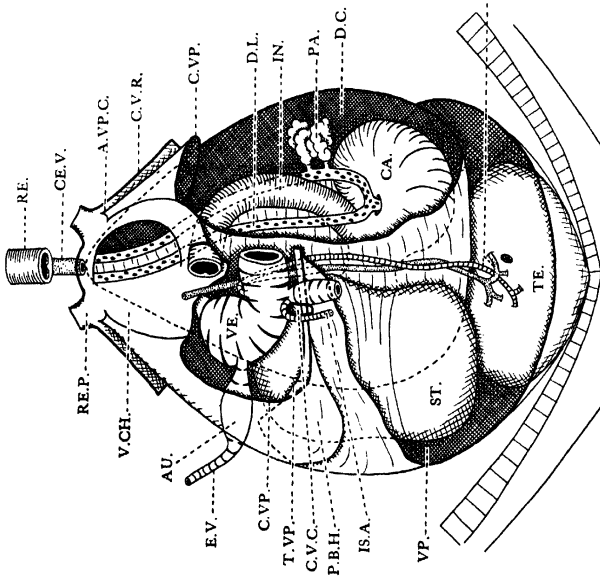

FIG. 21

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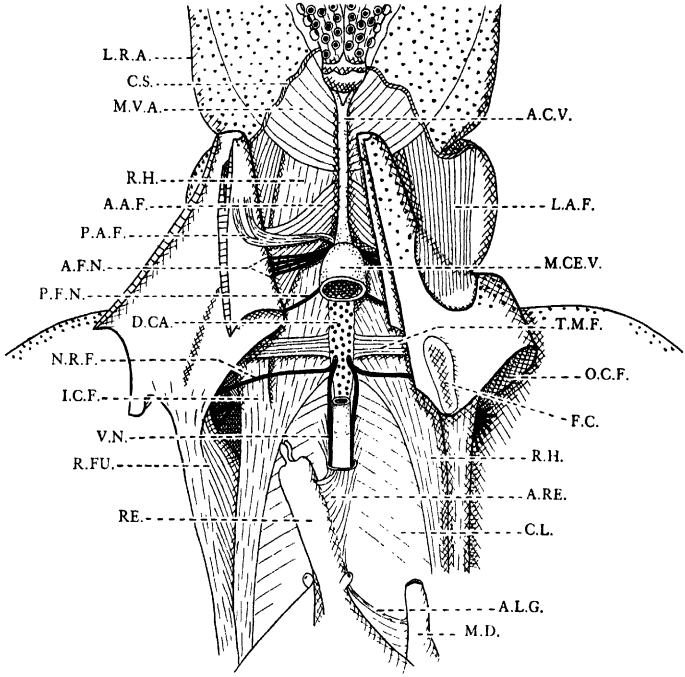

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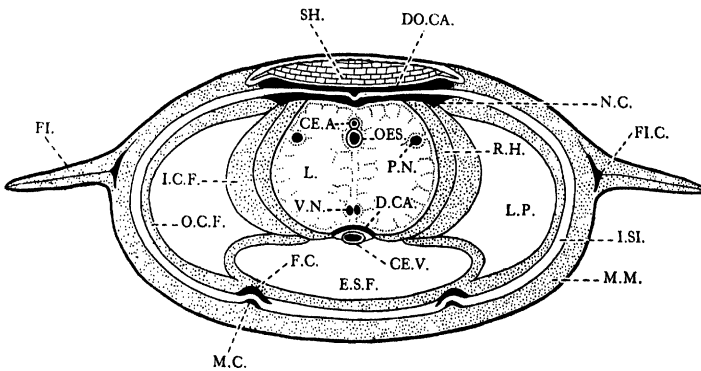

FIG. 24.

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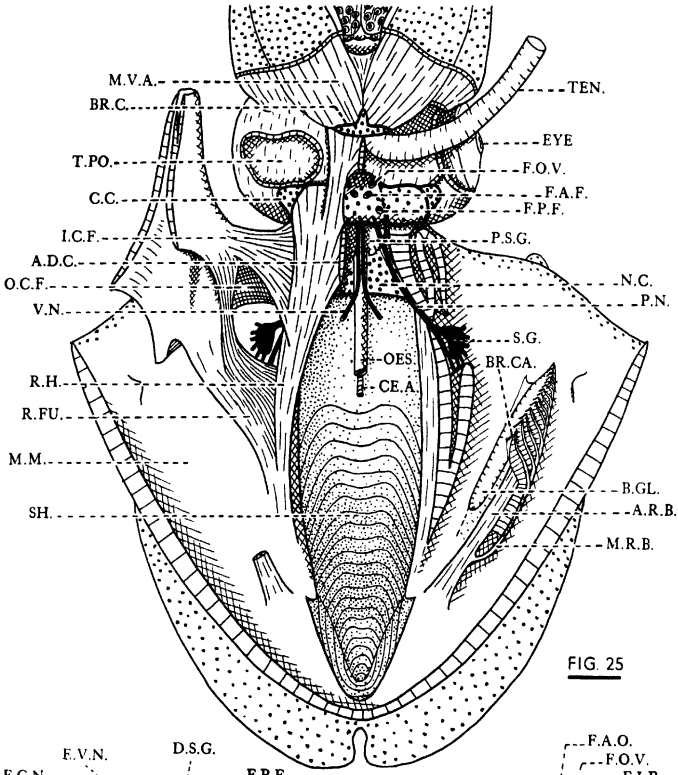


FIG. 25

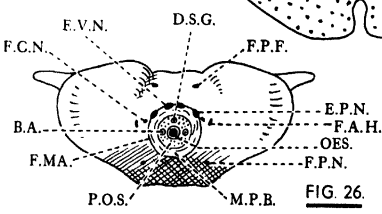
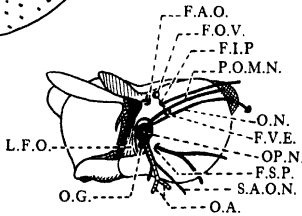


FIG. 26.



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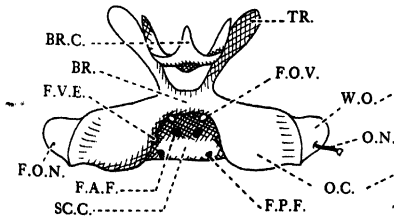

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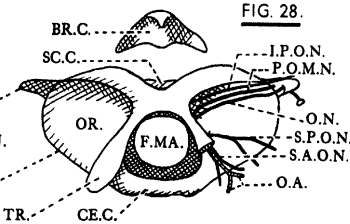

FIG. 29.

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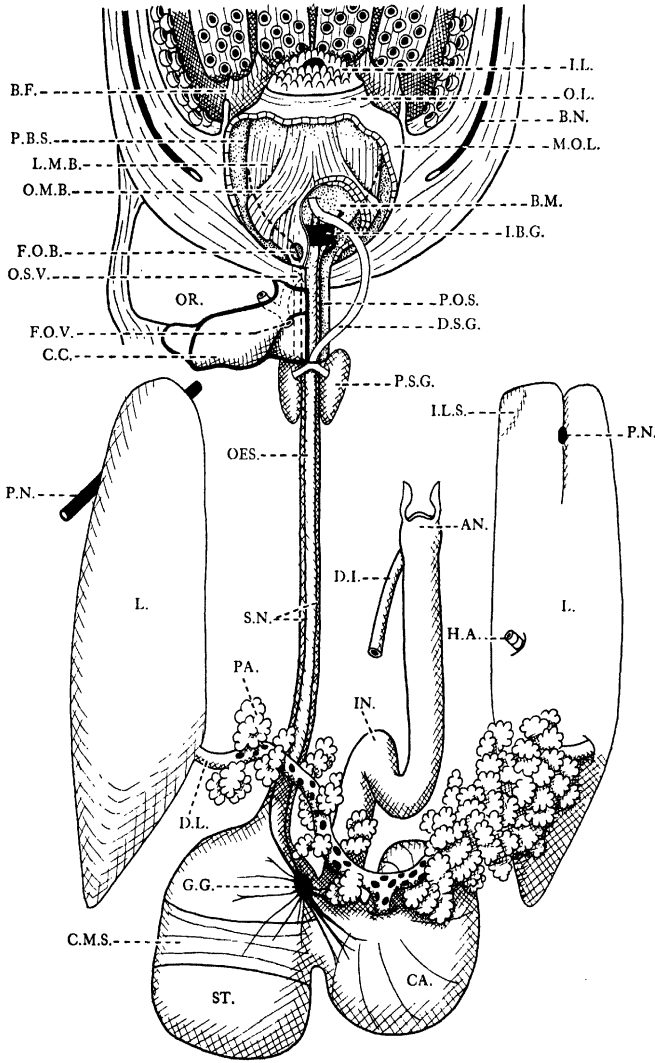

FIG. 36.

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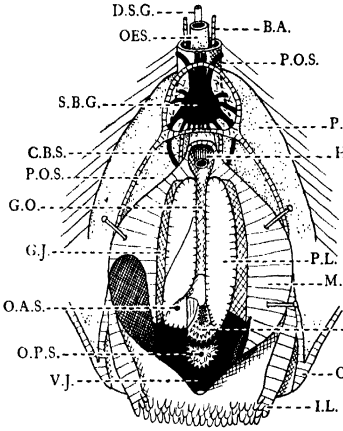

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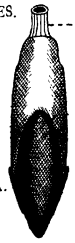

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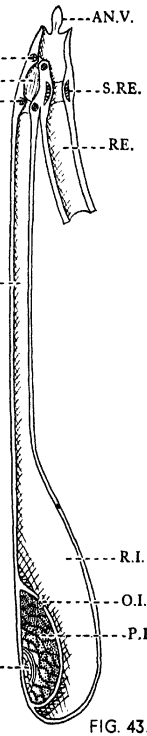

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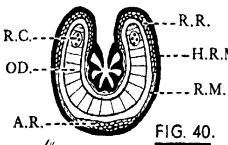

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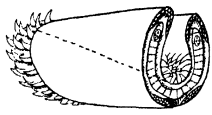
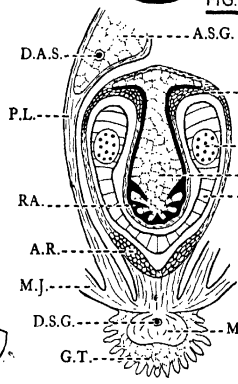


FIG. 39.

FIG. 42.



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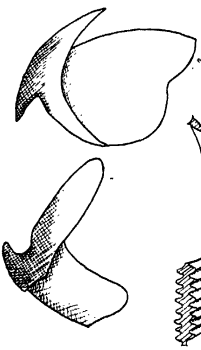

FIG. 44.

FIG. 45.

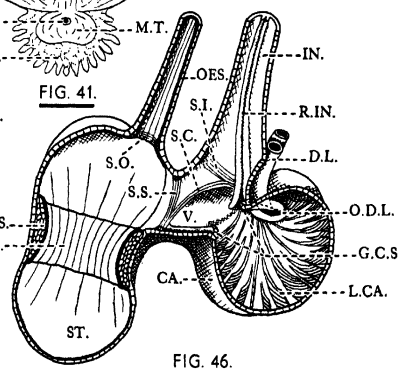

FIG. 46.

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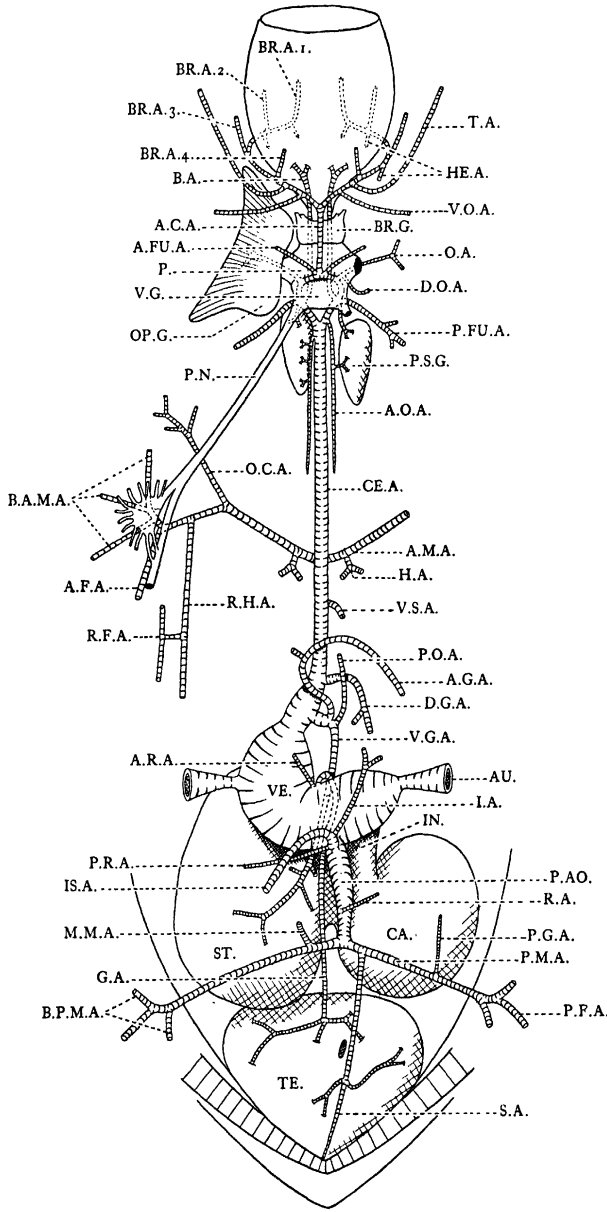

FIG. 47

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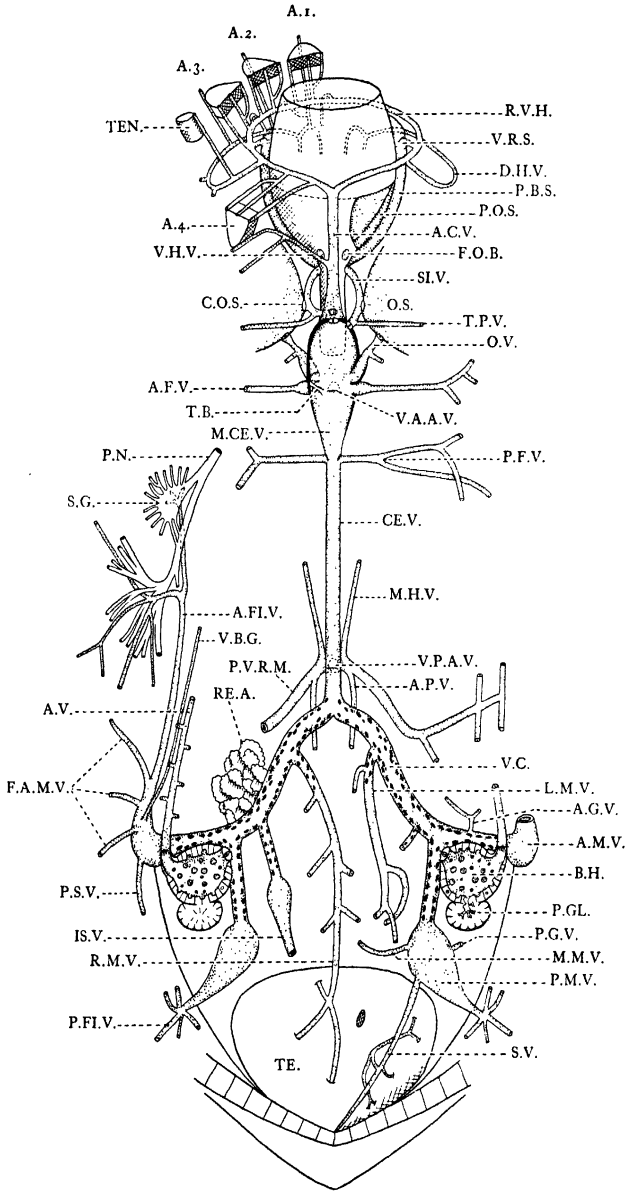

FIG. 48.

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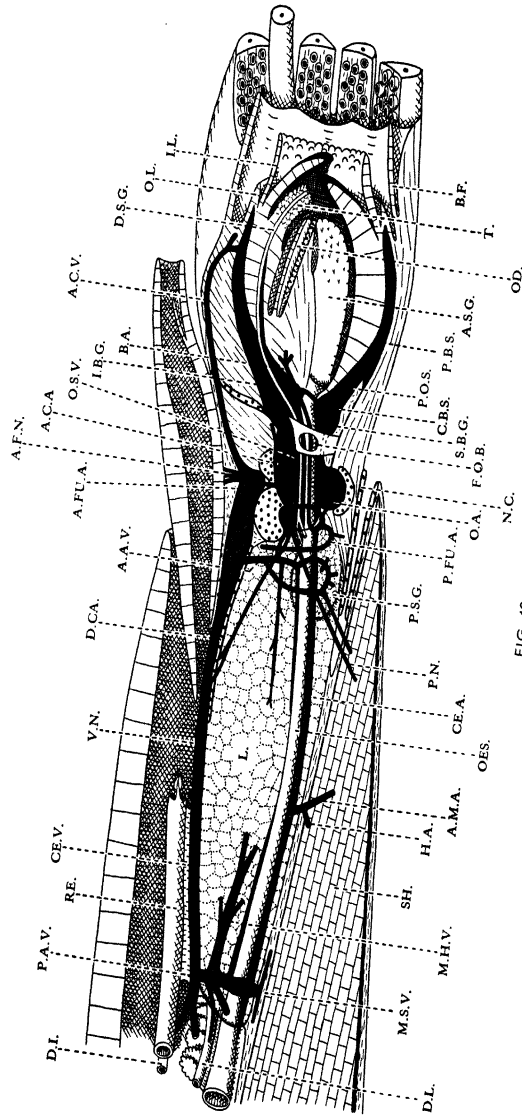

FIG 49

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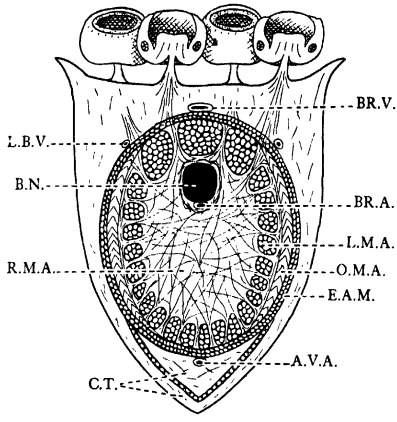

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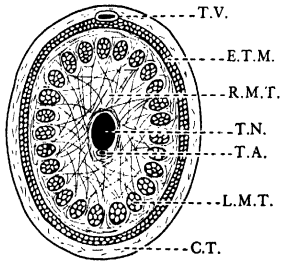

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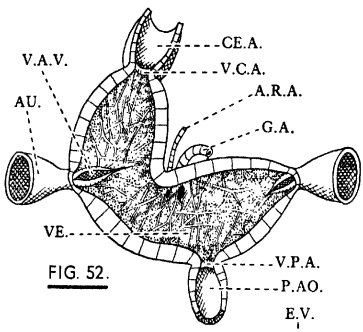


FIG. 52.

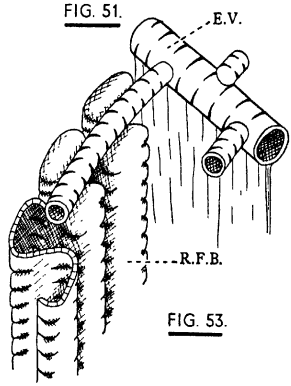


FIG. 53.

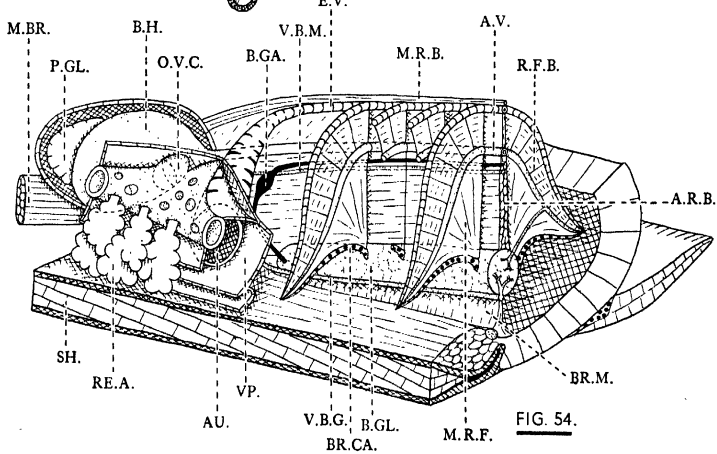


FIG. 54.

D.H.T. del

SEPIA

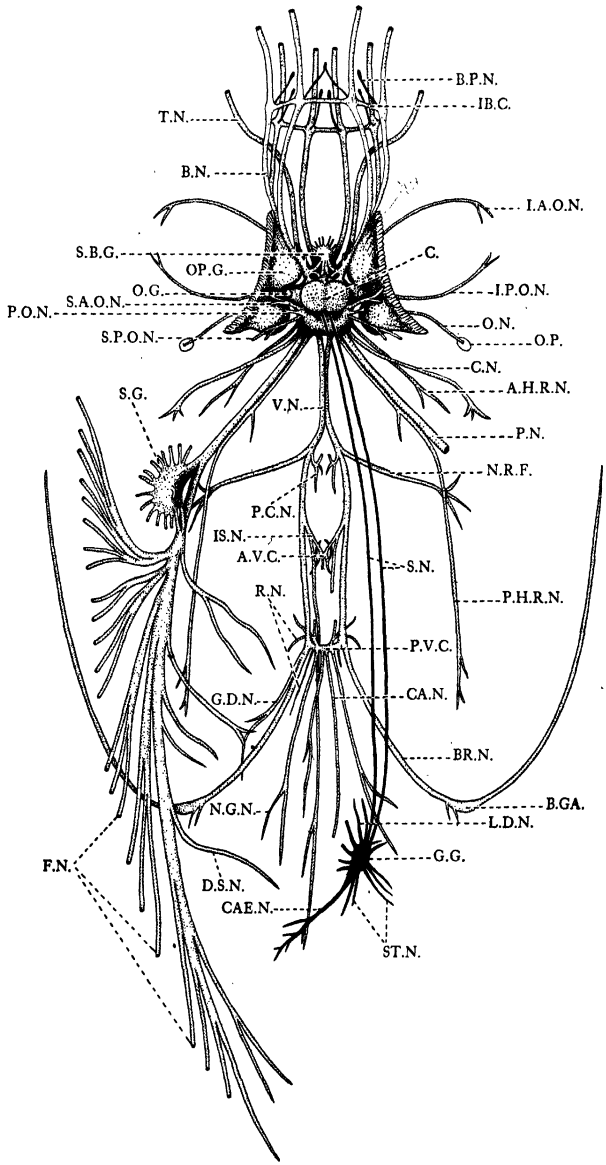


FIG. 55.

D.H.T. del

SEPIA

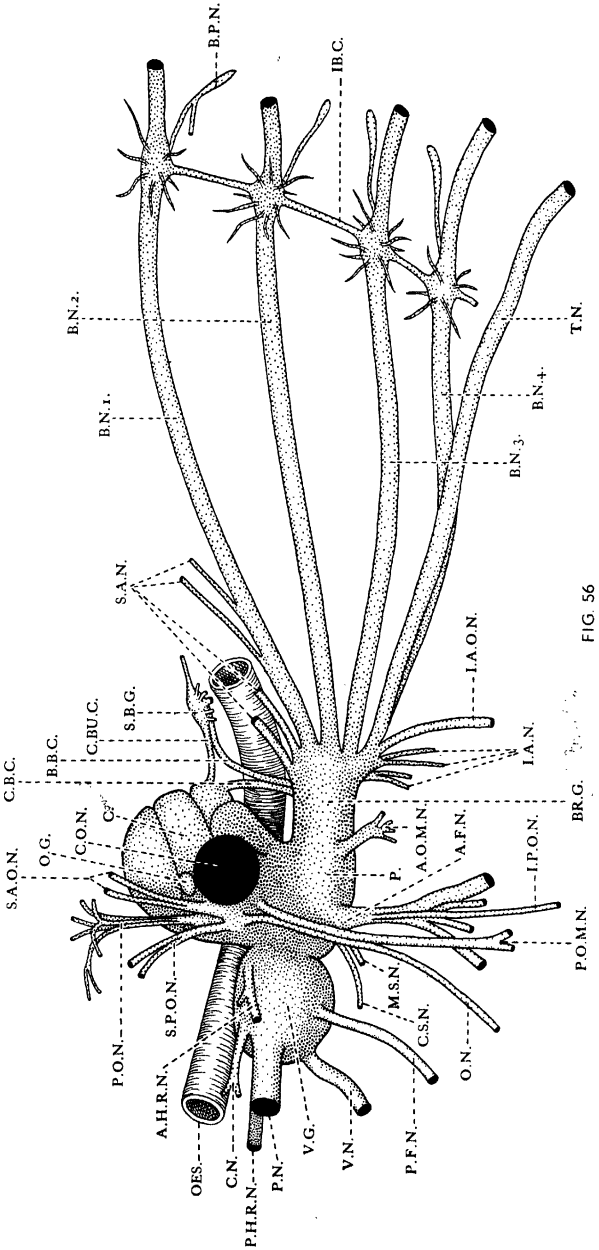


FIG. 56

D.H.T. del

SEPIA

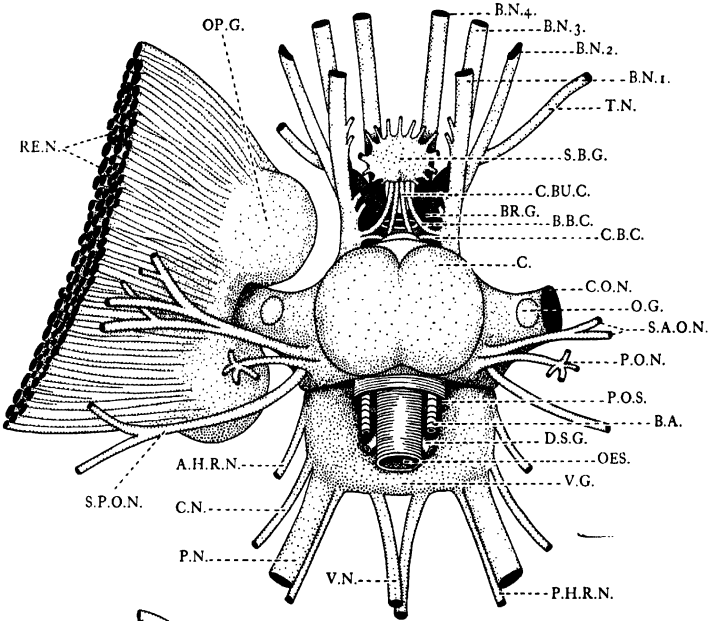


FIG. 57.

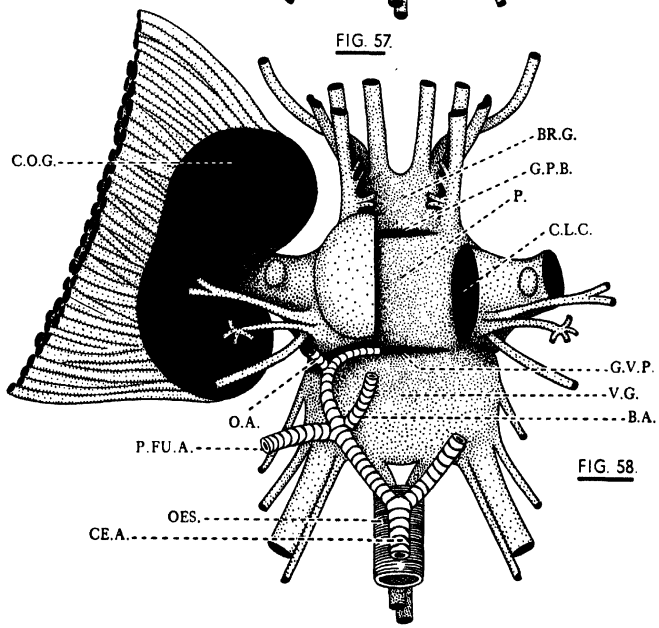


FIG. 58.

D.H.T. del

SEPIA

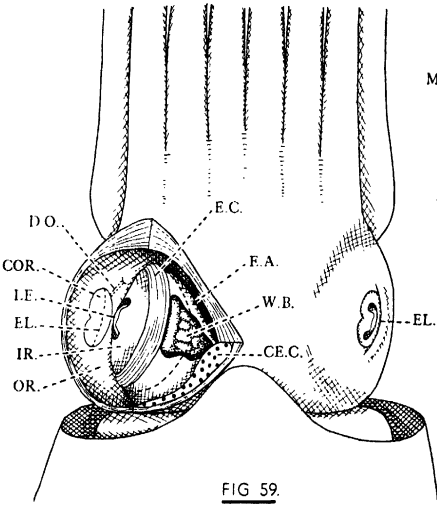


FIG. 59.

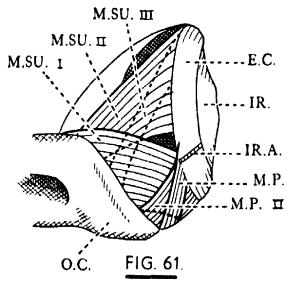


FIG. 61.

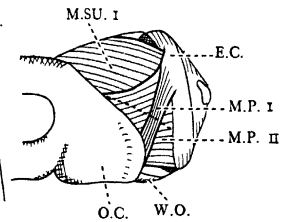


FIG. 62.

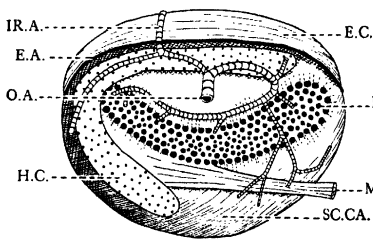


FIG. 60.

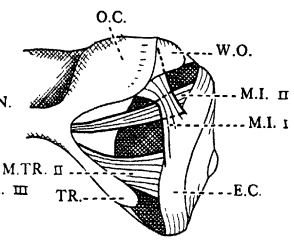


FIG. 63.

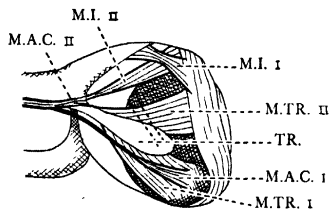


FIG. 64.

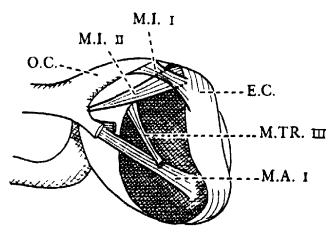


FIG. 65.

D.H.T. del

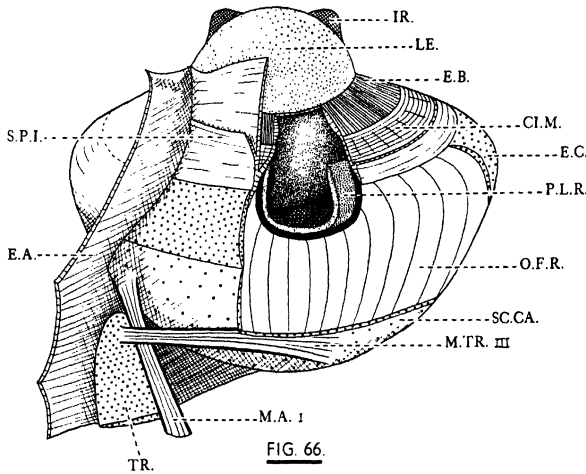


FIG. 66.

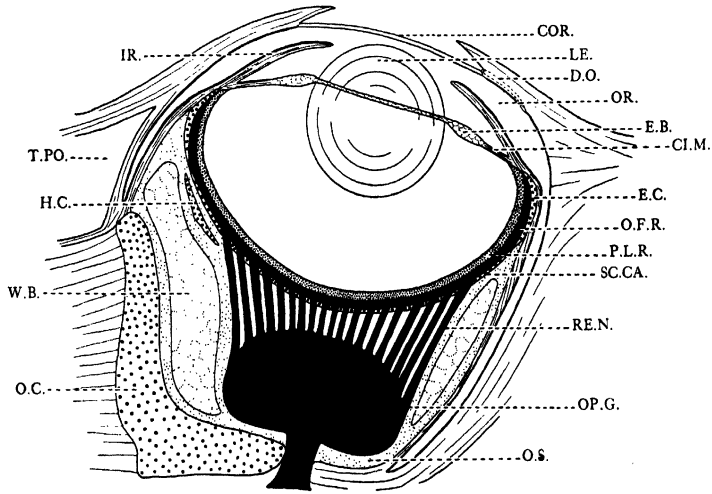


FIG. 67.

D.H.T. del

SEPIA

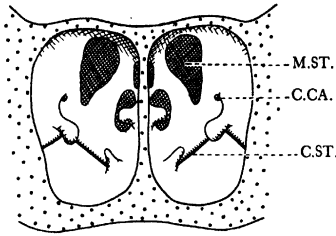


FIG. 68.

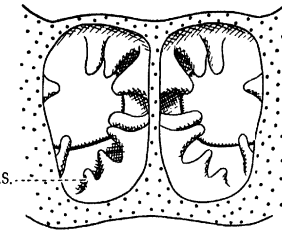


FIG. 69.

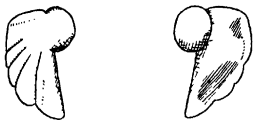


FIG. 70.

FIG 73.

FIG. 72.

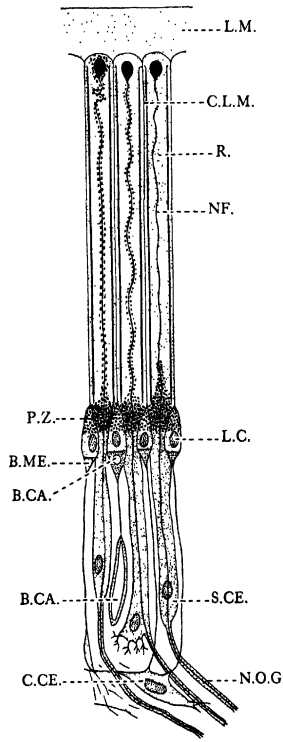
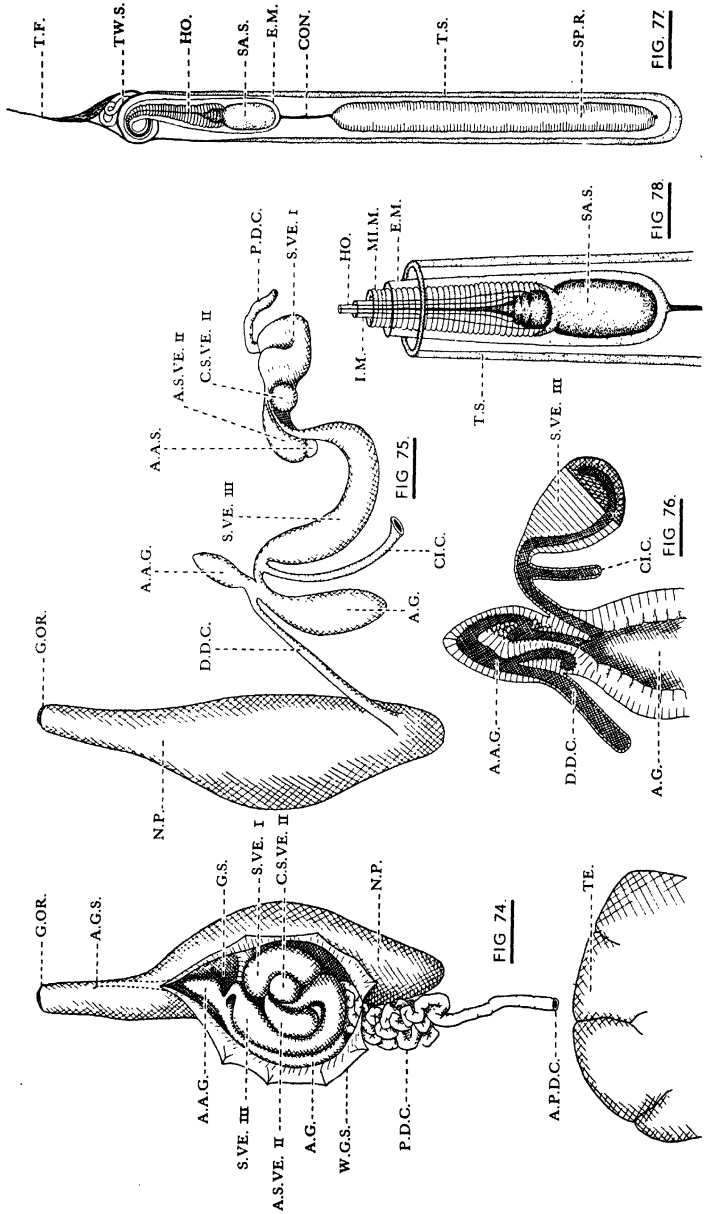


FIG. 71.

D.H.T. del

SEPIA



D.H.T. del

SEPIA

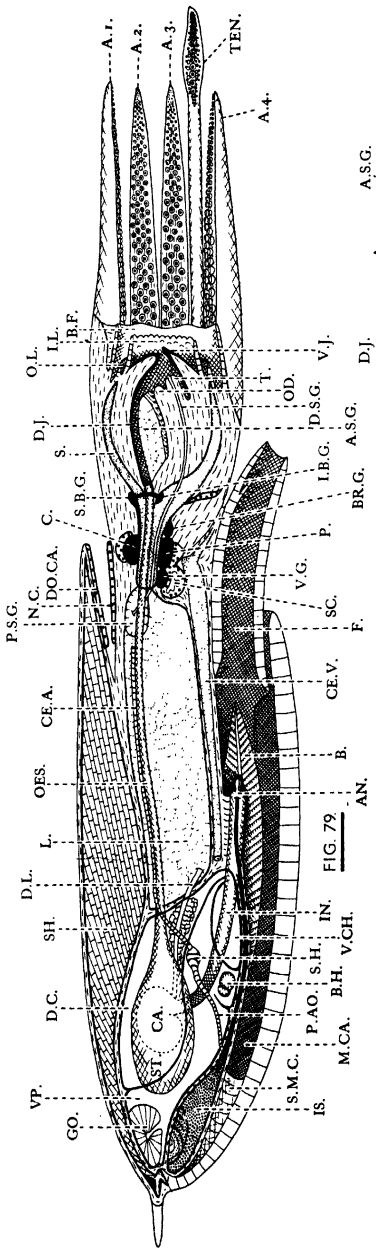


FIG. 79

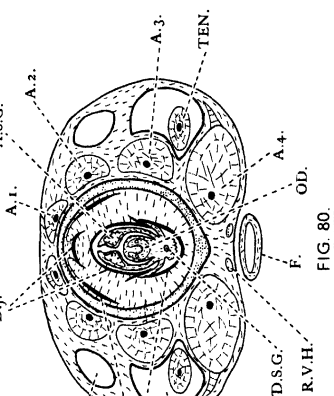


FIG. 80

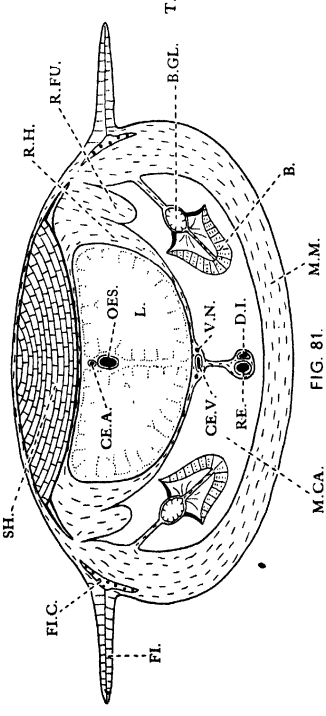


FIG. 81

J. & W.H.T. del

SEPIA